UNIVERSITY OF ALBERTA

REDESCRIPTION OF PONTOSAURUS LESINENSIS AND THE EVALUATION OF DOLICHOSAUR INTERRELATIONSHIPS AND PALEOECOLOGY

by

STEPHANIE ELAINE PIERCE ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Systematics and Evolution

DEPARTMENT OF BIOLOGICAL SCIENCES

Edmonton, Alberta
Spring 2003

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Degree: Master of Science

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Redescription of Pontosaurus lesinensis and the evaluation of dolichosaur interrelationships and paleoecology submitted by Stephanie Elaine Pierce in partial fulfillment of the requirements for the degree of Master of Science in Systematics and Evolution.

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ABSTRACT

Pontosaurus lesinensis is redescribed and phylogenetically analyzed. The redescription highlights new anatomical features that were not identified in the original study. A cladistic analysis finds Pontosaurus to be closely related to other dolichosaur species. An extensive phylogenetic study on dolichosaur interrelationships is also conducted. The results support earlier assertions that dolichosaurs are a non-monophyletic group that form successive sister taxa to snakes. Thus, it appears as though snakes are nested deeply within a radiation of elongate, limb reduced, marine squamates. In addition, the paleoecology of dolichosaurs is investigated. A geological and paleobiological analysis finds dolichosaurs to be a geographically widespread group of marine squamates that inhabited both near shore and offshore environments. They were predatory animals that fed on a variety of relatively small marine vertebrates and invertebrates. Their anatomy suggests that they were anguilliform swimmers that ambushed their prey by either foraging within small crevices or utilizing a predatory strike.

ACKNOWLEDGEMENTS

I would first and foremost like to extend a special thanks to Dr. Michael W. Caldwell (supervisor) for providing me with the opportunity to embark on this journey. I appreciate the time you spent with me pondering dolichosaur anatomy and phylogeny and I am grateful for the countless manuscripts you have read and edited for me. I will never forget the fun times we shared during fieldwork in Argentina and Saskatchewan. Thanks for being both my mentor and my friend.

I thank the members of my graduate committee, Dr. Brian D. E. Chatterton and Dr. Mark V. H. Wilson, for their advice and comments on my thesis research.

I am indebted to my father Dr. W. David Pierce for his everlasting moral and financial support. His patience, inspiring words of wisdom, and thought-provoking questions are forever ingrained into my 'memory'.

I am grateful to Jeroen Daniels for his continued love and moral support. I also acknowledge his assistance in constructing figures for my thesis; his artistic abilities and knowledge of Adobe Photoshop are insurmountable. I am also grateful for his willingness to listen to my trials and tribulations.

I thank Dr. F. Stojaspal from the Austrian Geological Survey in Vienna for assistance in obtaining permission to prepare and study the holotype of Pontosaurus lesinensis. I also thank Dr. J. D. Scanlon for translating the following articles from German to English: Kornhuber (1873), Kramberger (1892), and Nopsca (1903; 1908; 1923).

I offer thanks to my lab mates Lisa Budney, Timon Bullard, Alex Dutchak, Gavin Hanke, Chelsea Hermus, Al Lindoe, and Craig Scott, for their friendship, advice, and

enthusiasm. Additionally, I would like to thank Al Lindoe for his countless hours of delicate preparation and Gavin Hanke for providing me with access to his comparative library.

I am thankful to my family (Dad, Mom, John, Katherine, Shaelyn, Kyle, Dale, and Lara) and my close friends (Emily, Jeroen, Karleigh, Rob, and Sean) for their unconditional love and moral support, even though they have no idea what I do. I am also grateful for all of the fun times and countless memories we have shared together.

Financial support for this study was provided by: National Sciences and Engineering Research Council (NSERC) operating grant to Dr. Michael W. Caldwell, two Province of Alberta Scholarships granted to the author, and by graduate teaching assistantships from the Department of Biological Sciences, University of Alberta, granted to the author. Partial funding for this study was also provided by a number of small scholarships administered through the University of Alberta and the Government of Alberta.

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GENERAL INTRODUCTION

INTRODUCTION TO THESIS

Dolichosaurs are a group of small, long-necked, marine lizards. They appear in the fossil record during the Late Cretaceous (Cenomanian-Turonian), a time characterized by an extensive radiation of marine squamates, including the eel-like limbed snakes (pachyophiids), the medium-sized aigialosaurs, and the large mosasaurs. Dolichosaurian fossil remains have been discovered in sediments from Europe, the Middle East, and North America. Currently, the family Dolichosauridae is composed of eight identified species and one unnamed taxon; however, the majority of the species are known from only one specimen. Their general morphology consists of a small head, more than 10 cervical vertebrae, reduced limbs, and an oar-like tail. Dolichosaurs have long been suggested to be closely related to mosasauroids (mosasaurs and aigialosaurs) and possibly even the closest relatives to snakes (Kramberger, 1892; Nopcsa, 1903, 1908, 1923).

Since their initial discovery in the late 19th century, dolichosaurs have remained largely unstudied (Owen, 1850; Meyer, 1860; Seeley, 1881; Kornhuber, 1873; Kramberger, 1892; Nopcsa, 1903, 1908, 1923); however, with the renewed interest in the origins and evolution of snakes (see Coates and Ruta, 2000 for review), dolichosaurs are now being extensively re-examined in terms of anatomy and phylogeny. Over the past several years, three previously identified dolichosaur species and two new taxa have been thoroughly described (Dal Sasso and Pinna, 1997; Dal Sasso and Renesto, 1999; Caldwell and Cooper, 1999; Caldwell, 1999a, b; Caldwell, 2000; Lee and Caldwell, 2000). Results from the most recent cladistic study (Lee and Caldwell, 2000) suggest that dolichosaurs fall within the clade Pythonomorpha (mosasauroids and snakes) as

successive sister taxa to snakes. Consequently, the family Dolichosauridae appears to be a non-monophyletic assemblage.

My thesis research is designed to examine dolichosaur anatomy and interrelationships more closely. The thesis is divided into three chapters, each highlighting a different aspect of dolichosaurian evolution. Chapter One focuses on the detailed redescription of a poorly known dolichosaur Pontosaurus lesinensis (Kornhuber, 1873). Chapter Two investigates the interrelationships of the family Dolichosauridae to determine if the family is a monophyletic assemblage and whether dolichosaurs are more closely related to snakes than to other marine reptiles (mosasauroids). Chapter Three explores the geology and paleobiology of dolichosaurs. By undertaking this thesis, essential anatomical and phylogenetic information will be discovered. This study will not only expand our knowledge of dolichosaurs, but will also contribute to the resolution of snake origins.

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CHAPTER ONE

REDESCRIPTION AND PHYLOGENETIC POSITION OF PONTOSAURUS LESINENSIS (KORNHUBER, 1873)

Accepted as: Pierce, Stephanie E. and Michael W. Caldwell. 2002/2003. Redescription and phylogenetic position of the Adriatic (Upper Cretaceous; Cenomanian) dolichosaur Pontosaurus lesinensis (Kornhuber, 1873). Journal of Vertebrate Paleontology.

INTRODUCTION

Kornhuber (1873) described a new species of Cretaceous lizard from two separate, and what he concluded to be, reciprocally complete specimens found in the platy limestones outcropping on Hvar Island (=Isola di Lesina), Croatia. The first stone slab (slab A) was recovered in 1869 and contained the remains of a small reptile exposed in dorsal view. Nothing remained of the skull or cervical vertebrae, but the posterior portion of the skeleton, including the limbs was well preserved. The second stone slab (slab B) was discovered in 1870 and contained a skeleton of another small reptile, exposed in ventral view. This new specimen contrasted with the earlier one in that it retained the anterior portion of the body including a skull and cervical vertebrae, but only traces of the forelimbs, and the dorsal vertebral column in front of the sacrum. Comparing the two slabs, Kornhuber determined that the anatomical features agreed with each other in all respects and grouped them together to describe a single species: Hydrosaurus lesinensis.

Kornhuber's classification of this new taxon was based on superficial cranial similarities with the extant lizard genus Hydrosaurus (Wagler, 1830), now known as Varanus (Merrem, 1820), or the monitor lizard. However, upon later review by Kramberger (1892), it was determined that Hydrosaurus lesinensis shared more characteristics with the extinct Adriatic lizards Aigialosaurus (Kramberger, 1892), Adriosaurus (Seeley, 1881), and Acteosaurus (Meyer, 1860), than the recent genus Hydrosaurus. The result was that Kornhuber's species was renamed Pontosaurus lesinensis (Kramberger, 1892). In the same publication, Kramberger systematically

grouped P. lesinensis into the newly erected family, the Aigialosauridae (Kramberger, 1892), along with Aigialosaurus, Adriosaurus and Acteosaurus.

Nopcsa (1903) reevaluated the systematic position of P. lesinensis along with Dolichosaurus (Owen, 1850), Opetiosaurus (Kornhuber, 1901), Carsosaurus (Kornhuber, 1893), Mesoleptos (Cornalia, 1851), and the remaining 'aigialosaurs' discussed by Kramberger (1892). He pointed to similarities shared between Pontosaurus, Acteosaurus, Adriosaurus and the dolichosaur, Dolichosaurus, and emended the family Dolichosauridae (Gervais, 1852) to include all four genera. The remaining lizards discussed (Aigialosaurus, Opetiosaurus, Carsosaurus, and Mesoleptos) were grouped into the family Aigialosauridae based on comparable mosasauroid characteristics.

Except for brief mentions in comparative studies (Nopcsa, 1908;1923; Calligaris, 1987/1988; Rieppel, 1988; Dal Sasso and Pinna, 1997; Dal Sasso and Renesto, 1999) Pontosaurus has never once been reexamined in any detail. In fact, after Kornhuber's original paper both specimens of P. lesinensis were 'lost' to science as Kornhuber had never given a specimen number, nor designated a collection facility. But, in 1996, more than a century after it had been first described, M. Caldwell and M. Lee located the specimens assigned to P. lesinensis in the collections of the Austrian Geological Survey in Vienna.

Cursory observations of P. lesinensis indicated that slab A and slab B contained the remains of anatomically different animals, were poorly prepared, and had been inaccurately described in terms of osteological features. Consequently, slab B, containing the skull and the majority of diagnostic characters, was brought back to North America in 1999 for re-preparation and future study. Here, we redescribe the well

preserved anterior portion of P. lesinensis and present the results of a phylogenetic analysis to ascertain the systematic position of P. lesinensis among dolichosaurs, aigialosaurs, mosasaurs and other squamate groups.

OSTEOLOGICAL ANALYSIS

Kornhuber (1873) initially tried to prepare the slabs of rock containing Pontosaurus lesinensis by using a chisel, but found the rock to be too tough and the bone too brittle. He then resorted to chemical methods. First the specimen was bordered in wax and subjected to dilute and then concentrated acetic acid. He then attempted to prepare the bone with hydrochloric acid and later sulfuric acid, but the bone started to dissolve. Kornhuber, after his laborious efforts, became convinced that the skeleton could not be further prepared without jeopardizing the fossil itself. Unfortunately, the specimen was left with a coating of calcium carbonate that masked many of the anatomical features. Therefore, the specimen of P. lesinensis described here required a considerable amount of re-preparation, especially in the region of the skull, pectoral girdle, and limb before it could be redescribed.

Re-preparation started by subjecting the specimen to an air abrasive, using powdered dolomite. This method proved to be too coarse and resulted in the loss of the hyoid bones. Consequently, the remainder of the preparation was done using an air scribe and pin vice under a high powered microscope. To prepare the ventral (original) surface of the specimen the entire dorsal surface was stabilized with epoxy resin and fibreglass; this prevented the rock from cracking under the pressure of the air scribe. Following the completion of the ventral surface, the skull was covered with a layer of

water-soluble fish glue, a layer of fibreglass, and then a thin layer of epoxy. The dorsal surface of the skull was then prepared. After preparation was finished, a clear epoxy was used to fill in and stabilize the dorsal skull window in order to permit future examination of the skull elements. Subsequently, a margin was cut in the epoxy layer on the ventral surface and the slab of rock was soaked in water until the fish glue dissolved. The epoxy/fibreglass layer was then removed. Specimen drawings were made using a microscope with camera lucida attachment and photographs were taken with a digital camera fixed to a microscope.

INSTITUTIONAL ABBREVIATIONS

FMNH, Field Museum of Natural History, Chicago, Illinois, U.S.A.; GBA, Austrian Geological Survey, Wien, Austria; IRSNB, Institut de Recherches Scientifiques Naturelles de Belgique.

SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus, 1758
SQUAMATA Oppel, 1811
DOLICHOSAURIDAE Gervais, 1852

GENUS PONTOSAURUS (Kornhuber, 1873)

Type species—Pontosaurus lesinensis

Range—Upper Cretaceous; Cenomanian.

Junior Synonym—Hydrosaurus lesinensis

Revised Generic Diagnosis—A long and slender marine lizard possessing a unique supraoccipital-parietal articulation, with the supraoccipital resting on top of and forming

a v-shaped suture with the parietal; elongation of all postdentary bones; twelve cervical vertebrae; hypapophyses with large unfused peduncles on C2-C12; twenty-eight dorsal vertebrae; fused scapulocoracoid with a primary coracoid emargination.

PONTOSAURUS LESINENSIS (Kornhuber, 1873)

(Figs. 1-1–1-4)

Diagnosis—As for genus.

Type Locality—Hvar Island (= Isola di Lesina), 43°10′N, 16°30′E, Croatia, in the local Plattenkalken or platy limestones.

Holotype—GBA 1873/4/2 (Figs. 1-1–1-4) preserves the articulated cranial and postcranial remains of one individual. The entire skull and mandibles are represented. The postcranium is composed of twelve articulated cervical vertebrae, twenty-eight dorsal vertebrae, and the shoulder girdles and forelimbs.

Remarks—The second specimen (slab A) referred to Pontosaurus lesinensis is removed and here treated as cf. Dolichosauridae although we acknowledge similarities with aigialosaurs.

DESCRIPTION

Overall Impression

The specimen is fully articulated from the tip of the snout through the pectoral girdle and down to the 28th dorsal vertebra (Fig. 1-1A, B). However, the posterior elements, including the pelvic girdle (except for fragments), hind limbs and tail are not preserved. The specimen is exposed in ventral view, but a slight rotation of the cervical

vertebrae, right half of the skull and left and right mandibles has exposed several bones in medial, lateral and dorsal view. Preparation of the dorsal surface of the skull has revealed the remaining dorsal elements of the skull. The pectoral girdles and limbs are well exposed, although the left manus is not preserved.

Cranial elements

The skull and mandibles are long, smooth and slender with nearly all elements in their natural articulations (Figs. 1-2A, B, 1-3A, B). In ventral view, the right side of the skull and mandible have been rotated ventromedially exposing their lateral surfaces. In contrast, the left mandible is exposed in medial view. The basicranium is also preserved in ventral view and is in articulation with the atlas. In dorsal view, the left side of the skull is well preserved, while the right side is slightly disrupted. Only the posterior portion of the left mandible is observable. The back of the skull articulates caudally with the atlas and axis, the only two vertebrae visible in this view.

Snout—The premaxilla is an extremely small, single median element (Fig 1-2A, B). At its anterior tip, it is broad and flat. Beyond this point, the premaxilla constricts to form a long and thin narial bar similar to that of mosasauroids (Russell, 1967; Carroll and deBraga, 1992). The premaxilla-maxilla contact is uncertain because the right and left sides of the contact are very different. The anterior portion of left side fits snugly against the maxilla; in contrast, the anterior portion of the right side is free and does not contact the maxilla, a similar condition to Adriosaurus (Lee and Caldwell, 2000). At its posterior extent, the premaxilla becomes sandwiched between a pair of nasal bones situated along

its lateral borders. In this respect, the nasals restrict the premaxilla's contribution to the external narial opening and seem to prevent its contact with the frontal bone, a scenario consistent with all squamates except mosasauroids (Russell, 1967; deBraga and Carroll, 1993). The premaxillary teeth are not exposed.

The maxilla is a long, broad element that was identified, but not described, by Kornhuber (1873) (Figs. 1-2A, B, 1-3A, B). It reaches its maximum thickness more than halfway down the bone's extent and tapers into a thin wedge both anteriorly and posteriorly in a configuration similar to that of varanids (Estes et al., 1988) and mosasauroids (Russell, 1967; Carroll and deBraga, 1992; deBraga and Carroll, 1993). Anteriorly, the maxilla is sutured to the premaxilla and forms one half of the external narial opening. Posteriorly, the dorsal margin of the maxilla is slightly concave and articulates with the prefrontal in an extensive sutural contact. The thin posterior process of the maxilla supports the anterior process of the jugal. Three maxillary foramina can be observed on the anterior portion of the maxilla.

On the ventral margin of the right maxilla approximately ten teeth can be identified (Fig. 1-3A, B). Although most of the anterior teeth have been crushed and broken the posterior teeth are well preserved displaying a sharp triangular appearance like those of Varanus (Estes et al., 1988) on top of high pedestals or a bulbous mass of ossified tissue as in mosasauroids (Russell, 1967; Carroll and deBraga, 1992; deBraga and Carroll, 1993; Caldwell et al., 2002). The teeth also manifest a laterally compressed and weakly re-curved enamel-dentine crown with superficial grooves or fluting.

Kornhuber (1873) reported a trace of the right lacrimal posterodorsal to the maxilla and anterior to the jugal. This area is composed entirely of the prefrontal with no

evident trace of the lacrimal. In fact, it is unclear whether a lacrimal was ever present; if absent it would match the condition in snakes, Pachyrhachis (Lee and Caldwell, 1998) and many other squamate groups (Estes et al., 1988).

Kornhuber (1873) described the jugal as an incomplete piece of projecting bone. However, the jugal, as now prepared, is a massive element (Figs. 1-2A, B, 1-3A, B). The anterior edge of the jugal arch extends forward to meet the prefrontal anteriorly and the maxilla ventrally; it does not extend anteriorly past the orbit as in mosasauroids (deBraga and Carroll, 1993). Posterodorsally, the jugal is large and curves gradually in an anterior direction to contact the lateral process of the postorbital.

The nasals are thin, flat and paired, resembling those of Halisaurus (deBraga and Carroll, 1993) (Fig. 1-3A, B). They are positioned on either side of the premaxilla framing the medial boarder of the external narial opening. Posteriorly, the nasals thicken slightly and become rounded to articulate with the frontal bone.

The prefrontal is long and broadens posteriorly as in mosasauroids (deBraga and Carroll, 1993), but is very different from the boomerang configuration observed in the dolichosaur Adriosaurus (Lee and Caldwell, 2000) (Figs. 1-2A, B, 1-3A, B). Anteriorly, it forms the posterolateral margin of the external narial opening. Its medial border conforms to and extends halfway down the lateral surface of the frontal. Its lateral border follows the maxilla below. Posteriorly, it forms the anterior margin of the orbit and accepts the jugal bone at its posterolateral tip. There is no evidence of contact with a lacrimal.

Skull Roof—The frontal is a long, flat element approximately one-third the length of skull (Fig. 1-3A, B). It generally resembles an hourglass in outline, being expanded at both its anterior and posterior ends and pinched at its mid-point, a configuration very similar to that in modern teiids (Estes et al., 1988). At its anterior border, the frontal has five processes: one large sagittal process, two large lateral processes, and two small parasagittal processes. The external edge of the lateral processes fits against the prefrontal, while the internal rim forms the posterior margin of the external narial opening. The remaining three processes receive the nasals. The median, sagittal process separates the nasals from one another, while the notches between the sagittal and parasagittal processes receive their articulating surfaces. At its midpoint, the frontal forms the dorsal margin of the orbit. The posterior border is simple and articulates with the parietal in a straight suture.

The postfrontal is a "large", boomerang-shaped element in dorsal view (Fig. 1-2A, B). It clasps both the frontal and parietal along its medial border and attaches to, but does not fuse with, the postorbital along its posterolateral surface. It frames the posterodorsal border of the orbit.

The parietal is a single, tabular bone, composing approximately one-third of the skull length (Fig. 1-2A, B). The parietal table is perforated by a large parietal foramen, which is situated well behind the frontal-parietal suture as in all mosasauroids (Russell, 1967; Carroll and deBraga, 1992; deBraga and Carroll, 1993). From here, the parietal table extends posteriorly in a long, pronounced, parietal crest [as seen in snakes and pachyophiids (Lee and Caldwell, 1998)], which contacts and disappears underneath the supraoccipital. The parietal wings are situated well below the surface of the parietal

table, are smooth and rounded along their lateral surfaces, and form the medial borders of the narrow supratemporal fenestra. Posteriorly, the parietal wings stretch out into two distinct suspensorial rami, which are bordered by the paroccipital process of the exoccipital-opisthotic medially, and the supratemporal laterally.

The postorbital is a thin band of bone that forms the anterolateral border of the supratemporal fenestra (Fig. 1-2A, B). At its proximal end, it articulates with, but does not fuse with, the postfrontal before it sends a stout jugular process ventrolaterally to meet the jugal bone. Posteriorly, the postorbital contacts the epipterygoid (a taphonomic artifact?) immediately prior to meeting the squamosal in an oblique suture.

The squamosal is a thin band of bone that forms the posterolateral border of the supratemporal fenestra (Fig. 1-2A, B). Anteriorly, it contacts the postorbital in an oblique suture. At its posterior tip, the squamosal contacts the quadrate laterally and the supratemporal medially.

The supratemporal fits securely on the lateral surface of the parietal ramus and the medial surface of the squamosal, in a manner comparable to the supratemporal in Varanus (Estes et al., 1988; deBraga and Carroll, 1993) (Fig. 1-2A, B). It is approximately the same width as the squamosal, but only about one-third the length. It extends slightly beyond the posterior limits of both the parietal and squamosal.

According to Kornhuber (1873), the skull preserves both quadrates somewhat out of place anteriorly and closer to the midline. Although Kornhuber was correct in the identification of the left quadrate, his right quadrate is actually part of the pterygoid. Re-preparation has subsequently exposed the right quadrate resting lateral to the right articular (Figs. 1-2A, B, 1-3A, B).

The quadrate is a backwards C-shaped structure comparable to that observed in mosasauroids (Russell, 1967; Carroll and deBraga, 1992; deBraga and Carroll, 1993), specifically Plioplatycarpus (per. obs. specimen # IRSNB 1673), and the teiid Dracaena (per.obs. specimen # FMNH 207657). The suprastapedial and infrastapedial processes are comparable in size and are separated from one another posteriorly by a narrow stapedial notch. The shaft is almost vertical with a strong lateral flange and the tympanic ala is deep. Dorsally, the quadrate is suspended from the squamosal, supratemporal, and the paroccipital process of the exoccipital.

Braincase—The basisphenoid is well preserved (Fig. 1-3A, B). It possesses two large posteroventrally directed basal tubera that were identified as the pterygoid processes by Kornhuber (1873). It cannot be determined, with any certainty, how much of the basisphenoid contributes to the basal tubera because the suture between the basisphenoid and basioccipital has been obliterated. The basipterygoid processes are visible anterior to the tubera and articulate with the pterygoids laterally not anterolaterally as in many squamates (Estes et al., 1988). The parasphenoid process is not exposed.

The basioccipital is a flat, rectangular element that has been broken in the midline (Fig. 1-3A, B). Its contribution to the basal tuber cannot be determined. Additionally, the occipital condyle is not observable.

The supraoccipital has a rectangular base and a clover-shaped anteromedial shelf (Fig. 1-2A, B). The 'stem' and the two lateral 'leaves' of the shelf rest on top of, and form a v-shaped suture with, the parietal; this configuration comes close to that of snakes, but the supraoccipital in snakes never sits above the parietal. Instead the supraocciptial in

snakes is level with and slight on-lapped by the parietal. The third medial 'leaf' forms a crest that runs down the center of the supraoccipital's rectangular base. The rectangular base gradually slopes caudally underneath the parietal until it unites with the atlas posteriorly, a configuration that typifies non-snake squamates (Estes et al., 1988). On its lateral margin the supraoccipital meets the left and right exoccipital in a straight, anterior-posterior directed, suture.

The exoccipital is broad along its contact with the supraoccipital (Fig. 1-2A, B, 1-3A, B). It rests below the level of the supraoccipital and underneath the parietal. It is sutured to the supraoccipital and does not contact its conterpart above the foramen magnum. The exoccipital bears a large, oval paroccipital process ventrally. The contact with the prootic is not visible.

Palate—Both pterygoids were described by Kornhuber (1873) as having their anterior parts sutured to the palatines and ectopterygoids and with a pronounced furrow on the ventral surface for vessels and nerves. Closer inspection of the pterygoids reveals that Kornhuber's palatines are actually the anterior palatal rami of the pterygoid bones (Fig. 1-3A, B).

The pterygoid, as exposed, is a long, broad, edentulous element. The palatal rami are separated from each other by a very narrow interpterygoid vacuity resembling that of mosasaurs (Russell, 1967) and various other squamates (Estes et al., 1988). Posterolaterally, the palatal ramus is perforated by a large foramen and attaches to the ectopterygoid along with the quadrate ramus. The quadrate ramus meets the basipterygoid process of the basisphenoid approximately at its mid-point and the quadrate

at its posterior end. A long, shallow, furrow is also evident running down the middle of the quadrate ramus.

Kornhuber's (1873) identification of the left ectopterygoid is correct, but in ventral view it is poorly preserved (Fig. 1-3A, B); it surrounds the junction between the palatal ramus and quadrate ramus of the pteryoid. However, there is a bone on the dorsal surface that appears to be the remaining portion of the left ectopterygoid (Fig. 1-2A, B). It is a long columnar element that is lying dorsal to the jugal and is in contact with the maxilla anteriorly.

The epipterygoid is a simple, broad, columnar element (Fig. 1-2A, B). It does not appear to be in its nature articulation. The dorsal tip is situated on the postorbital bone directly in front of the postorbital-squamosal suture. The ventral tip ends just prior to the mandible below. The epipterygoid extends and scarcely decreases in size ventrocaudally.

Two long, narrow and somewhat weakly curved hyoid bones (presumably the first ceratobrachials) are visible behind the skull. Kornhuber (1873) originally identified these bones as the quadratojugals, but also made an attempt at identifying them as the columellae (stapes), postfrontals, and squamosals. They are comparable to the first ceratobrachials illustrated for Heloderma (Estes et al., 1988), being narrow anteriorly and broad posteriorly.

Mandible—The dentary is a long, shallow, element (Fig. 1-3A, B). Anteriorly, the dentary is slender and is characterized by a smooth anterior symphysis; this suggests that the contact between the dentaries was loose and mobile and similar to that of mosasauroids, pachyophiids, and snakes (Lee et al., 1999). Posterior, the dentary ends in

an undulating suture with the surangular and overlaps the splenial below. The medial surface is characterized by an extensive ventrally placed Meckel's groove. Re-preparation has revealed a number of isolated teeth associated with the dentary. They are morphologically similar to the maxillary teeth (i.e., laterally compressed, sharp, and weakly recurved with shallow furrowing). Furthermore, there is no indication of a labial wall on the medial surface of the dentary; this suggests that the alveolar bone forms a three-sided dental alveolus lined with a partial cribiform plate as in aigialosaurs and other dolichosaurs (Caldwell et al., 2002).

In lateral view, the splenial bulges beneath the dentary (Fig. 1-3A, B). Anteriorly, the splenial thins and disappears onto the medial surface of the dentary. Posteriorly, the splenial thickens and displays a central indentation that surrounds the angular in a ball-and-socket articulation similar to that observed in mosasauroids (Russell, 1967; Carroll and deBraga, 1992; deBraga and Carroll, 1993; Polcyn et al., 1999), dolichosaurs (Dal Sasso and Pinna, 1997; Caldwell, 1999a; 1999b; 2000), pachyophiids (Lee and Caldwell, 1998; Lee et al., 1999), and snakes (for a contrary view on the homologies in this region, see Rieppel and Zaher, 2000).

In medial view, the splenial expands dorsally to cover the dentary. Its anterior tip is narrow and follows the Meckel's groove below. Poteriorly, the splenial expands over the dentary and articulates with the surangular and articular in an undulating contact. Posterodorsally, the splenial is perforated by a large foramen.

The coronoid is visible only in medial view (Fig. 1-3A, B), and rests on top of the surangular. Its anterior process is long and projects slightly beyond the surangular,

barely contacting the splenial below; its ventral margin is somewhat convex. A small coronoid process appears at its posterior extent.

The angular is a splint of bone that is bulbous anteriorly and thin posteriorly (Fig. 1-3A, B). Anteriorly, it rests within the concavity of the splenial forming the posterior half of the ball-and-socket articulation. In medial view, the anterovental margin of the angular is perforated by a small foramen. Its dorsal margin is capped by the surangular laterally and the articular medially.

The lateral surface of the surangular is large, rectangular in outline, and tapers into a small wedge of bone posterodorsally (Fig. 1-3A, B). Its anterior contact with the dentary is narrow and undulating. There is a slight indentation on the anterodorsal surface for the reception of the coronoid. A small foramen is situated on its posterodorsal tip.

In medial view, the surangular appears small and narrow. Its anterior tip is lost beneath the coronoid. The adductor fossa is narrow, long and located behind the coronoid and in front of the articular cotyle. The surangular contributes to the anterior portion of the articular cotyle.

There is no apparent suture separating the prearticular and articular, they are one continuous, compound bone (Fig. 1-3A, B). This type of fusion is also displayed in mosasauroids (Russell, 1967; deBraga and Carroll, 1993; Polcyn et al., 1999). Anteriorly, the articular is narrow, sandwiched between the surangular above and the angular below, and contacts the splenial in an undulating suture. Posteriorly, the articular widens and forms the articular cotyle for the reception of the quadrate. It terminates in an expanded retroarticular process.

Postcranial elements

With the exception of the atlas and axis, the postcranial elements are only visible in ventral view (Figs. 1-1A, B, 1-2A, B, 1-4A, B, 1-5A, B). The cervical vertebrae have undergone a slight twisting to the left revealing some anterolateral structures. The dorsal vertebrae are all articulated to their adjacent ribs. The left pectoral girdle is well preserved and has rotated laterally revealing its ventral surface. The right pectoral girdle is exposed in ventral view and is compressed onto the underlying cervical vertebrae. Both forelimbs are in place, but only the left manus is preserved. The manus is slightly longer and wider then the propodial and epipodials combined.

Vertebral Column— Kornhuber (1873) identified a total of nine cervicals, but what he thought was the atlas-axis complex is actually C3. Furthermore, based on morphology and the position of the pectoral girdle, what Kornhuber identified as the first two dorsals actually corresponds to the last two cervicals. Therefore, by making the appropriate changes the cervical count increases to twelve. In squamates, a cervical count greater than ten has only ever been observed in pachyophiids (Lee and Caldwell, 1998; Lee et al., 1999) and dolichosaurs (Dal Sasso and Pinna, 1997; Caldwell, 2000; Lee and Caldwell, 2000).

The cervical vertebrae gradually increase in width and length caudally (Fig. 1-1A, B, 1-4A, B). The atlas intercentrum and the right neural arch along with the anterior portion of the axis centrum are clearly visible in dorsal view (Fig. 1-2A, B). The left neural arch of the atlas and the entire axis centrum are visible in ventral view (Fig. 1-1A, B). Prezygapophyses are present along the right side of C2-C12 situated across the

postzygapophyses of each preceding vertebra. Most of the corresponding right synapophyses have been sheared off except those on C7 and C11-C12. All of the left synapophyses are preserved. C2-C12 all possess hypapophyses and large unfused peduncles that decrease in size posteriorly, similar to mosasauroids (Russell, 1967; Carroll and deBraga, 1992; deBraga and Carroll, 1993) and the fossil snake Dinilysia (Caldwell and Albino, 2002) (Fig. 1-4). Each peduncular complex has been folded to the left and is lying on the left synapophysis of the succeeding vertebral body. The axis has only one peduncular complex preserved, the posterior one. Long cervical ribs appear on C10 and C11, but are not discernible on any of the other cervical vertebrae.

Kornhuber (1873) counted thirty dorsals, but with the refinement in the cervical region the actual dorsal count is twenty-eight, for a total of 40 presacral vertebrae. The dorsal vertebrae are larger than the cervicals in both width and length and are more robustly ossified (Fig. 1-1A, B; 1-4A, B). There is a gradual increase in size posteriorly until the 25th dorsal, with the 26th –28th dorsals slightly decreasing in proportions. The ventral profile of the dorsal vertebra is wedge or T-shaped, an appearance caused by the proximal placement of the synapophyses; a similar vertebral profile is also observed in aigialosaurs (Carroll and deBraga, 1992; Polcyn et al., 1999), dolichosaurs (Caldwell, 1999b; Caldwell, 2000) and snakes. A procoelous pattern can be assumed based on a slight indentation on the anterior surface of the centra coupled with a posterior expansion or convexity. There is a firm articulation between each vertebra, therefore, the presence of zygosphenes and zygantra cannot be determined.

All dorsal vertebrae support ribs attached to the anteriorly positioned synapophyses. The ribs increase in size and thickness along with the vertebral column

until the 21st dorsal. The 22nd- 28th ribs decrease in size and thickness posteriorly. The ribs branch off from the centra in a narrow downward arch and then fold towards the mid-line forming a somewhat laterally constricted frame. Slightly obscuring the left side of the body and overlaying ribs 19-28 are remnants of digested gut contents.

The vertebral column has been broken along what appears to be the last dorsal vertebra; consequently, there is no evidence of sacral vertebrae. However, there are fragments of the left first and second sacral ribs lying behind the last dorsal vertebra (Fig. 1-1A, B). The sacral ribs are short, stout and straight. The first rib has a hook-like process at its distal tip; this feature is not preserved on the second rib, which has has a slightly expanded distal tip.

Shoulder Girdle and Forelimb—The scapula and coracoid are reduced in size and appear to be fused into a single scapulocoracoid element similar to that of the aigialosaur Opetiosaurus (Carroll and deBraga, 1992; deBraga and Carroll, 1993) (Fig. 1-4A, B). The scapular portion is small and is not emarginated. As in mosasaurs (Russell, 1967; DeBraga and Carroll, 1993), Haasia (Polcyn et al., 1999), and Aphanizocnemus (Dal Sasso and Pinna, 1997), the coracoid portion is significantly larger, possesses an anterior (primary) emargination and a fan-like posterior margin. A single coracoid foramen is also evident across from the glenoid fossa.

The interclavicle is present as a narrow horizontal bar lying between C11 and C12 (Fig. 1-4A, B). Although significantly smaller, its shape is very similar to the thin, flat interclavicle of Clidastes (Russell, 1967).

The propodial and epipodials are comparable to those observed in the dolichosaur Adriosaurus (Lee and Caldwell, 2000) (Fig. 1-4A, B). The humerus is a short element, slightly constricted mid-shaft and expanded at both ends. Both the ectepicondylar and entepicondylar foramina are absent. Proximally, there is a stout crest for the attachment of the pectoralis muscle. Distally, there is a large bulbous capitulum and a flat troclea; although the dimensions are smaller, the distal epiphysis resembles that of Opetiosaurus (deBraga and Carroll, 1993) and Haasia (Polcyn et al., 1999).

The epipodials are of similar size and are distally divergent; this distal divergence is observed in most mosasauroids (Russell, 1967; Carroll and deBraga, 1992) and the dolichosaur Adriosaurus (Lee and Caldwell, 2000). The radius is a simple rod-like structure that is slightly curved distally and articulated with the capitulum of the humerus above. The ulna is thick proximally, marginally decreasing in width distally. The olecranon is present and curves around the trochlea of the humerus. The distal epiphysis is well developed and articulates with the pisiform laterally.

The carpals are crushed laterally, but well preserved medially (Fig. 1-4A, B). Directly distal to and in contact with the ulna is the pisiform. Just below the ulna sits the large ulnare that articulates with either the intermedium or lateral centrale; however compared to aigialosaurs, which have a very small intermedium (Caldwell, 1996), this bone is more likely to be the lateral centrale. Carpals four and five are also visible just above the fourth and fifth metacarpal. The remaining carpals have been taphonomically fused together and cannot be discriminated.

All five metacarpals are present (Fig. 1-4A, B). The first and fifth are both shaped like an hourglass. Metacarpal two, three, and four are long and fairly straight.

All are positioned close to each other except for metacarpal five, which is situated at some distance from metacarpal four.

The phalangeal formula appears to be 2-3-4-5-3, a count that is primitive for all lepidosauromorphs (Carroll, 1988) (Fig. 1-4A, B). However, some of the phalanges have become taphonomically fused together and are overlapping each other. The shortest finger is the first, while the longest is the fourth. The terminal unguals are claw-like and pointed.

PHYLOGENETIC ANALYSIS

Of the squamate synapomorphies recognized by Estes et al. (1988), Pontosaurus possesses the following: reduced nasals, transverse frontoparietal suture, angular not reaching mandibular condyle, single headed ribs, cervical intercentra form prominent hypapophyses, loss of entepicondylar foramen in humerus, enlarged distal epiphysis of ulna, loss of gastralia, proatlas absent, premaxillae fused, parietal fused, jugal forms anteroventral border of orbit, procoelous vertebrae, dorsal intercentra lost, and an anterior coracoid emargination.

Accordingly, the phylogenetic relationship of Pontosaurus was examined by integrating the detailed osteological description presented here into a modified version of Lee and Caldwell's (2000) phylogenetic analysis of squamates (a modified analysis of Lee, 1998). Lee and Caldwell's (2000) squamate data matrix was selected because it is currently the only available data set that includes dolichosaurs. However, because this analysis is not intended to resolve global squamate relationships, all non-anguimorph squamate families were excluded. Therefore, the analysis presented here only includes

the Anguidae (outgroup), Xenosaurus, Shinisaurus, Heloderma, Lanthanotus, Varanus, and the recently described (or re-described) marine squamates: mosasaurids, aigialosaurids (Carroll and DeBraga, 1992; DeBraga and Carroll, 1993), Pachyrhachis (Lee and Caldwell, 1998), Pachyophis (Lee et al., 1999), Aphanizocnemus (Dal Sasso and Pinna, 1997), the Dolichosauridae [which includes Dolichosaurus and Coniasaurus (Caldwell, 1999; 2000; Caldwell and Cooper, 1999)], Adriosaurus (Lee and Caldwell, 2000), and Pontosaurus (this study).

Pontosaurus was coded for 159 of the 258 osteological characters (Appendix 1) used by Lee and Caldwell (2000). Character codings for all previously analyzed squamates follow Lee and Caldwell (2000) with some corrections as noted under the relevant sections. Cladograms were generated by subjecting the assembled character matrix to the Branch-and-Bound algorithm used in the computer software application PAUP Version 4.0b10 (Swofford, 2002). All characters were analyzed unordered and without character weight assignments as Lee and Caldwell (2000) found no difference in results between ordered and unordered states. Polymorphism in terminals was interpreted as 'uncertainty regarding the primitive state' when calculating tree lengths.

Cladistic analysis of the data matrix (Appendix 2) resulted in 3 shortest cladograms (334 steps) with a Consistency Index (C.I.) of 0.78, a Homoplasy Index (H.I) of 0.42, and a Retention Index (R.I.) of 0.81. The strict consensus/50% majority-rule consensus tree is shown in Figure 1-5. The clades Varanoidea and Pythonomorpha remain constant and displaying the same topology (except for Pontosaurus) resolved by Lee and Caldwell (2000). In terms of Pontosaurus, results indicate that it is a dolichosaur

nested within the clade Pythonomorpha as the sister taxon to Adriosaurus and the Ophidia.

DISCUSSION

The phylogenetic analysis presented here supports Nopcsa's (1903) claim that Pontosaurus is more closely related to other dolichosaurs than to aigialosaurs (Kramberger, 1892) or the modern genus Varanus (Kornhuber, 1873), and further reinforces the assertion that dolichosaurs are the sister group to all modern and extinct snakes (Nopcsa, 1908; 1923; Lee and Caldwell, 2000). However, the analysis also suggests that the family Dolichosauridae [including the Dolichosauridae (Dolichosaurus and Coniasaurus), Aphanizocnemus, Adriosaurus, and Pontosaurus from this study] is a paraphyletic assemblage. This apparent paraphyly is extremely problematic considering dolichosaurs have been hypothesized to be the sister group of snakes.

The paraphyly of the Dolichosauridae could be a consequence of the taxa and/or characters used in this analysis. First, there are nine known species of dolichosaurs, but only six were incorporated into the above analysis. A detailed re-examination of all known dolichosaur material including Acteosaurus tommasinii (Meyer, 1860), Acteosaurus crassicostatus (Calligaris, 1993), and Eidolosaurus trauthi (Nopcsa, 1923) would be desirable in order to determine the viability of the family. Second, the current analysis may lack phylogenetically informative dolichosaur characters. In this sense, the determination of more robust characters is required before dolichosaur phylogeny can be conclusively ascertained.

What is ultimately needed is a detailed examination and test of the monophyly of the Pythonomorpha (mosasaurs, aigialosaurs, dolichosaurs, pachyophiids, and snakes). Rieppel and Zaher (2000) recently re-examined Lee's (1998) character evidence in support of a monophyletic Pythonomorpha. Their analysis found pythonomorphs to be non-monophyletic, with the Mosasauroidea nested within varanoids and snakes nested with a clade including amphisbaenids and dibamids; all of these squamates were found to be anguimorphs. Although Rieppel and Zaher (2000) used the results of their analysis to reject Lee's (1998) assertion of a monophyletic Pythonomorpha, they did not accept their own phylogenetic tree as an accurate representation of squamate relationships; this makes their 'falsification' questionable. A critical review of the character codings used in this study and those employed by Rieppel and Zaher (2000) along with an additional analysis including all known pythonomorphs is necessary to resolve the monophyly of the Pythonomorpha. A rigorous analysis of mosasaurs, aigialosaurs, dolichosaurs, pachyophiids, and snakes might alter both our understanding of pythonomorph phylogeny and by extension snake origins.

FIGURE 1-1. Holotype, Pontosaurus lesinensis, GBA 1873/4/2. **A**, Photo; **B**, interpretive drawing. Abbreviations: c2–2nd cervical vertebra; c12–12th cervical vertebra; d1–1st dorsal vertebra; d28–28th dorsal vertebra; dgc–digested gut contents; sr1-2–sacral ribs 1 and 2. All other structures are labelled in the illustrations of each region (see Figs. 1-2–1-4). Scale bar = 50mm.

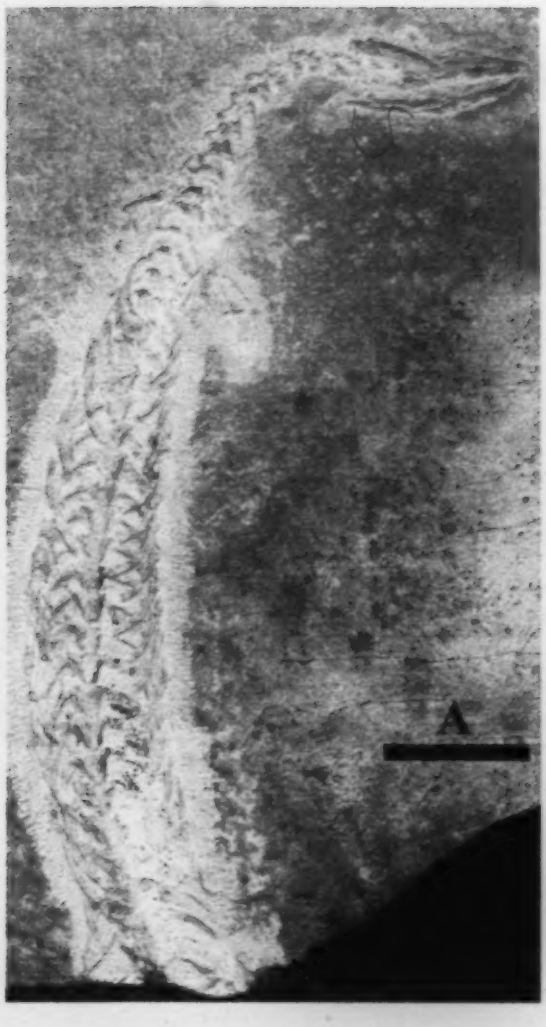
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FIGURE 1-2. Pontosaurus lesinensis, details of the dorsal skull. **A**, Photo; **B**, interpretive drawing. Abbreviations: ai–atlas intercentrum; an–atlas neural arch; ax–axis; ec–ectopterygoid; ep–epipterygoid; f–frontal; j–jugal; mx–maxilla; n–nasal; p–parietal; pf–postfrontal; pm–premaxilla; po–postorbital; popr–paroccipital process of the exoccipital; prf–prefrontal; q–quadrate; so–supraoccipital; sq–squamosal; st–supratemporal; sur–surangular. Scale bar = 10mm.

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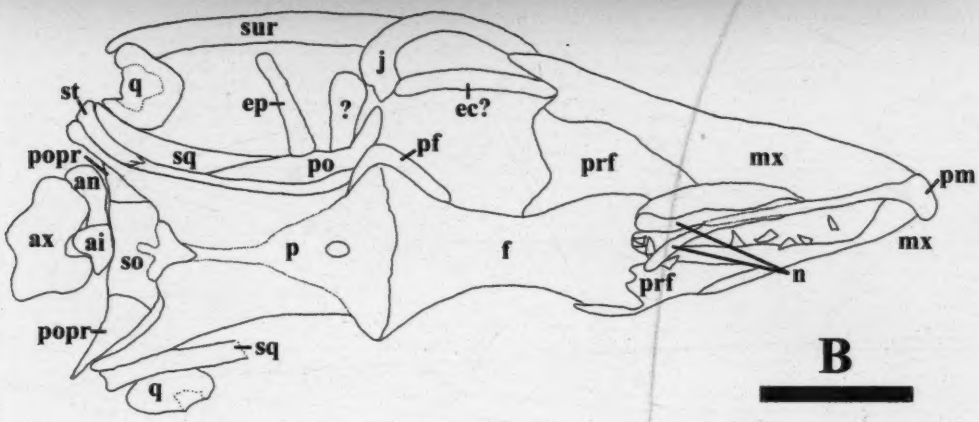
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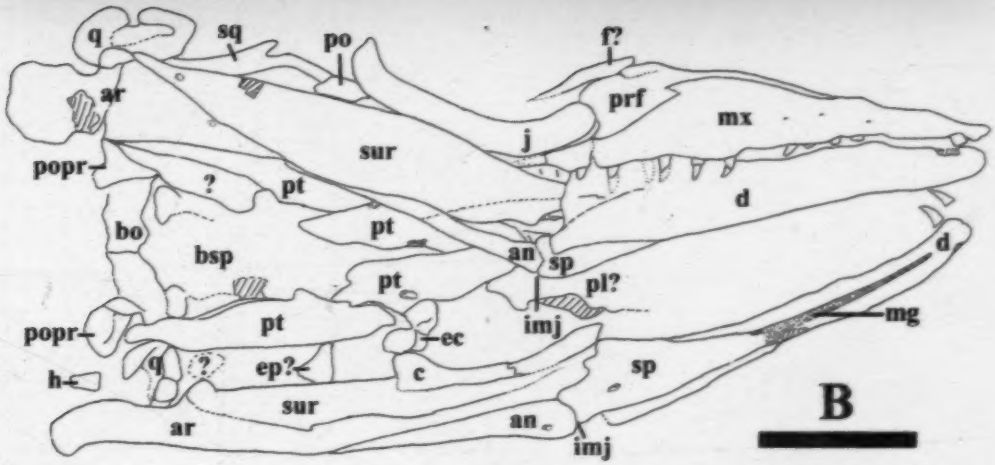
FIGURE 1-3. Pontosaurus lesinensis, details of the ventral skull. **A**, Photo; **B**, interpretive drawing. Abbreviations: an–angular; ar–articular (fused with prearticular); bo–basioccipital; bsp–basisphenoid; co–coronoid; d–dentary; ec–ectopterygoid; ep–epipterygoid; f–frontal; h–hyoid; imj–intramandibular joint; j–Jugal; mg–Meckel's groove; mx–maxilla; popr–paroccipital process of the exoccipital; pl–palatine; po–postorbital; prf–prefrontal; pt–pterygoid; q–quadrate; sp–splenial; sq–s quamosal; sur–surangular. Scale bar = 10mm.

A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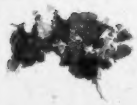


FIGURE 1-4. Pontosaurus lesinensis, details of the posterior cervicals (5-12), pectoral girdle and limb. **A**, Photo; **B**, interpretive drawing. Abbreviations: c5–5th cervical; c12–12th cervical; d6–6th dorsal; hu–humerus; ic–interclavicle; in/lc?–intermedium or lateral centrale; mc 1–metacarpal 1; ped– peduncle on hypapophysis; pis–pisiform; pzy–postzygapophysis; przy–prezygapophysis; ra–radius; sco–scapulocoracoid; syn–synapophysis; ul–ulna; uln–ulnare. Scale bar = 10mm.

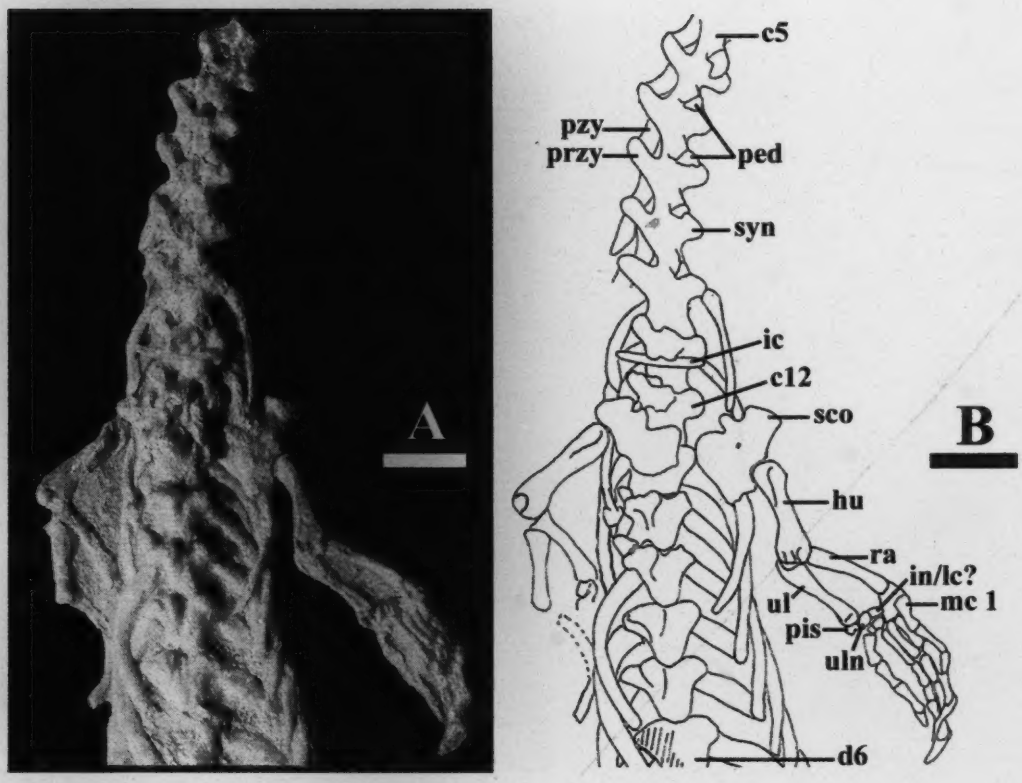
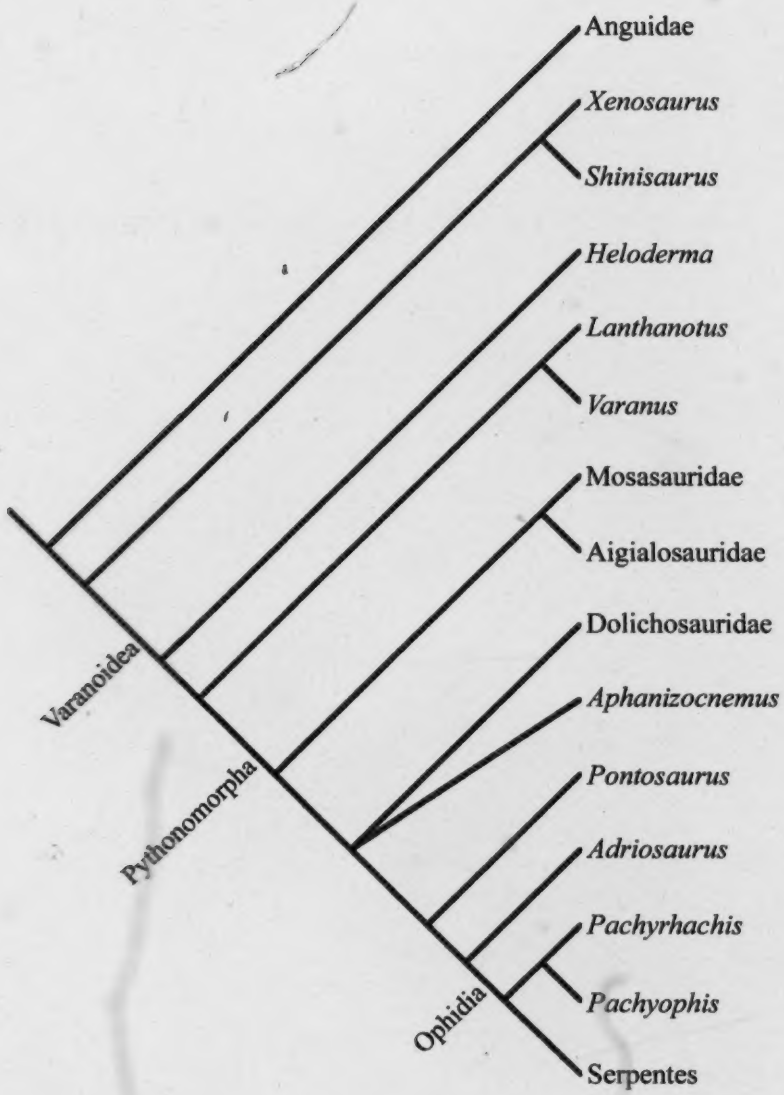

A
B
c5
pzy
przy
ped
syn
ic
c12
sco
hu
ra
in/lc?
mc 1
ul
pis
uln
d6

FIGURE 1-5. The phylogenetic position of Pontosaurus within the Anguimorpha, based on a cladistic analysis of 159 osteological characters, with all multistate characters unordered. The cladogram present here is the strict consensus/50% majority-rule consensus tree of 3 shortest trees (length = 334, consistency index = 0.78, homoplasy index = 0.42, retention index = 0.81). See text for details.


Anguidae
Xenosaurus
Shinisaurus
Heloderma
Lanthanotus
Varanus
Mosasauridae
Aigialosauridae
Dolichosauridae
Aphanizocnemus
Pontosaurus
Adriosaurus
Pachyrhachis
Pachyophis
Serpentes
Varanoidea
Pythonomorpha
Ophidia

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APPENDIX I

Character List

The data matrix used in this cladistic analysis. Most characters were discussed in Lee (1998) and Lee and Caldewell (2000) and are only briefly listed here. However, some codings were changed and are discussed under the relevant characters. The character number in brackets refers to the character number as listed by Lee and Caldwell (2000).

(a) skull roof

1(2). **Premaxilla**- Does not contact frontals (0); contacts frontals (1)

2(3). **Premaxilla with median palatal ramus bearing foramina**- Absent (0), present (1).

3(4). **Premaxillary lateral foramina**- Absent (0); present (1).

4(5). **Premaxilla-maxilla contact**- Immobile and sutural (0); mobile and non-sutural (1).

5(8). **Dorsal process of maxilla**- On middle or anterior end of maxilla (0); on posterior half of maxilla (1).

Pachyrhachis has been recoded from state 0 to state 1 as the dorsal process is positioned slightly posteriorly (Lee and Caldwell, 1998).

6(10). **Posterior process of maxilla**- Long, reaching or extending past middle of ventral margin of orbit (0); short, not reaching middle of ventral margin of orbit (1).

7(11). **Lacrimal**- Present, either permanently separate or fusing with prefrontal

during ontogeny (0); absent, never present as a discrete element (1).

8(13).**Lacrimal foramen**- Single opening (0); double opening (1).

9(15).**Snout shape**- Relatively short, rounded (0); long and very narrow, tapering to point (1).

10(18).**Jugal**- Does not extend anteriorly past orbit (0); extends anteriorly past orbit (1).

11(19).**Jugal**- With large posterior process (0); without large posterior process (1).

12(20).**Jugal**- Lacking dermal sculpture (0); with dermal scultpure (1).

13(21).**Nasals**- Large (0); greatly reduced or absent (1).

14(22).**Nasals**- Paired elements (0); single median element (1).

15(24).**External naris**- Not retracted, prefrontal and frontal both excluded from posterior narial margin by nasal and maxilla (0); slightly retracted, prefrontal (but not frontal) enters posterior narial margin (1); greatly retracted, prefrontal and frontal enter posterior narial margin (2).

16(26).**Antorbital ridge**- Absent (0); present, extending anteriorly from dorsal margin of orbit (1).

17(27).**Frontals**- Single median element (0); paired elements (1).

18(28).**Frontal**- Enters orbital margin, prefrontal does not contact postfrontal or postorbital (0); excluded from orbital margin, prefrontal contacts postfrontal or postorbital (1).

19(29).**Frontals**- Lateral orbital margin deeply concave (0); lateral orbital margin straight or only very slightly concave (1).

Not applicable in taxa where the frontal does not enter the orbit.

20(31).**Frontoparietal suture**- In dorsal view, simple straight transverse contact (0); in dorsal view, complex curved or interdigitating contact (1).

21(34).**Postfrontal** (or dorsomedial portion of single posterior orbital bone)- Forked medially, with an anterior process along the frontal and a posterior process along the parietal (0); not forked medially, does not extend a long distance along frontal or parietal (1).

22(35).**Palpebral** (superciliary) **ossifications on dorsal margin of orbit**- Present (0); absent (1).

23(36).**Postorbital**- Present (0); absent (1).

24(37).**Postorbital ventral process**- Small, forming less than half of posterior orbital margin, postorbital primarily a temporal bone (0); prominent, forming half or more of posterior orbital margin, postorbital primarily an orbital bone (1).

25(38).**Posterior margin of orbit**- Present and continuous (0); present but with small gap (1); very incomplete, less than 50% of posterior orbital margin bordered by bone (2).

26(42).**Pineal foramen**.- Present (0); absent (1).

27(44).**Parietal table and jaw adductor muscles**- Parietal table moderately wide, jaw adductors extend onto lateral margin only of dorsal surface of parietal (0); parietal table very wide, jaw adductors restricted entirely to ventral surface of parietal (1); parietal table a narrow sagittal crest, jaw adductors extend over entire dorsal surface of parietal (2).

28(46).**Suspensorial ramus** (posterolateral process) **of parietal**- Well-developed (0); extremely short or absent (1).

29(47).**Upper temporal arch**- Complete, upper and lower temporal fenestrae separated (0); incomplete, upper and lower temporal fenestra confluent (1).

30(48).**Temporal arch**- Without canthal crest (0); with canthal crest (1).

31(51).**Dorsal process of Squamosal**- Absent (0); present (1).

32(55).**Supratemporal**- In deep position, on ventrolateral surface of parietal (0); in superficial position, on dorsolateral surface of parietal (1).

33(56).**Supratemporal**.- Confined to skull roof (0); forms part of paroccipital process and/or braincase (1).

34(57).**Supratemporal**- Small, less than half the maximum width of the skull (0); large, at least half the maximum width of the skull (1).

35(58).**Supratemporal-prootic contact**- Absent (0); present (1).

36(59).**Quadrate suspension**- Mobile, articulates dorsally with squamosal, supratemporal and opisthotic (0); mobile, articulates dorsally with supratemporal, little or no contribution from other elements (1); mobile, articulates dorsally with opisthotic, little or no contribution from other elements (2).

37(61).**Quadrate**- Tympanic crest (outer conch) directed laterally and a well-developed wall (0); tympanic crest directed laterally but a low ridge (1); distinct tympanic crest absent and external surface of quadrate only weakly concave (2).

38(63).**Quadrate shape**- Without large, posteroventrally curved, suprastapedial

process (0); with large, posteroventrally curved, suprastapedial process (1).

39(64).**Mandibular articulation of quadrate**- Saddle-shaped, with lateral and medial condyles (0); flat, a single continuous condyle (1).

(b) braincase and associated structures

40(67).**Ventromedial processes of frontals**- Not contacting anything below olfactory tracts (0); abutting or sutured with each other below olfactory tracts (1); contacting parabasisphenoid below olfactory tracts (2).

41(69).**Parietal downgrowths**- Absent or weakly developed ridges (0); prominent flanges (1).

42(71).**Parietal downgrowths**- Not sutured to prootic (0); Sutured to prootic (1).

43(72).**Parietal downgrowths**- Not contacting parabasisphenoid or orbitosphenoid (0); contacting parabasisphenoid (1).

44(73).**Optic foramina**- Not enclosed in bone (0); enclosed partly or entirely by frontals (1).

45(74).**Anterior brain cavity**- Not floored by bone (0); floored by large descending frontal flanges (1).

46(75).**Trigeminal foramen or foramina**- Anterior margin not enclosed in bone (0); anterior margin enclosed by descending flange of parietal (1).

47(78). **Crista prootica** (ridge on lateral surface of the prootic, overhanging foramen pro nervi facialis)- Well-developed lateral flange (0); reduced to weak ridge, or absent (1).

48(80).**Foramen pro nervi facialis**- Single (0); double (1).

49(85).**Basisphenoid**- Without long posterolateral flanges (0); with long posterolateral flanges (1).

50(86).**Basipterygoid process**- Long, i.e. projecting far antero-laterally beyond the body of the basisphenoid (0); short, i.e. not projecting very far beyond the body of the basisphenoid (1).

51(87).**Basal tubera**- Posteriorly located, very near to occipital condyle (0); anteriorly located, well away from occipital condyle (1).

52(88).**Posterior opening of vidian canal**- At basisphenoid-prootic suture (0); situated within basisphenoid (1).

53(89).**Posterior opening of vidian canal**- Situated anteriorly, well in front of the posterior end of the basisphenoid (0); situated posteriorly, near the posterior end of the basisphenoid (1).

54(90).**Opisthotic**- Flange extending between basal tubera and paroccipital process weak or absent, most of the stapes exposed in ventral view (0); wide horizontal flange extending posterolaterally from basal tubera to paroccipital process obscuring much of the stapes in ventral view (1).

55(91).**Supraoccipital**- Does not contact parietal, unossified gap persists between the two elements (0); abuts parietal, the two elements meet but contact is non-sutural, and a tiny gap might remain between the two elements along part of the dorsal edge of the supraoccipital (1); sutural contact with parietal, entire anterodorsal edge of supraoccipital contacts parietal (2).

56(92).**Supraoccipital**- Situated ventral or posteroventral to parietal, does not

form part of posterior skull roof (0); situated posterior to parietal, forms part of posterior skull roof (1).

57(95).**Posttemporal fenestra**- Present as an opening (0); completely closed via sutural contact of the skull roof and otic region of braincase (1).

(c) palate and associated structures

58(96).**Septomaxilla-maxilla contact**- Rigid, septomaxilla extensively sutured to the dorsal surface of the palatal flange of the maxilla (0); mobile, septomaxilla not sutured to maxilla (1).

59(98).**Median flange of septomaxilla**- Short, not reaching level of prefrontal (0); long, extends posteriorly to reach level of prefrontal (1).

60(100).**Opening of Jacobson's organ**- Enclosed fully by maxilla and vomer, sometimes with a tiny contribution from the septomaxilla, not confluent with choana (0); enclosed partly by maxilla and vomer, confluent posteriorly with choana (1); enclosed fully by vomer and septomaxilla only, not confluent with choana (2).

61(104).**Vomer**- Main portion plate-like (0); main portion rod-like (1).

62(105).**Vomer**- Anterior or anteromedial to palatine (0); entirely medial to palatine (1).

63(108).**Palatine-vomer contact**- Immobile, sutural contact (0); mobile, non-sutural contact (1).

64(109).**Palatine**- Long - as long as vomer (0); short - half as long as vomer (1).

65(111).**Palatine**- Without distinct medially-directed process (0); with distinct

rectangular process projecting medially from the middle portion of the palatine to the skull midline (1).

66(113).**Ectopterygoid**- Does not enter cheek (0); enters cheek as a sliver sandwiched between maxilla and jugal (1).

67(114).**Ectopterygoid-palatine contact**- Absent, maxilla enters suborbital fenestra (0); present, maxilla excluded from suborbital fenestra (1).

68(116).**Interpterygoid vacuity** ("pyriform recess" of Estes et al., 1988)- Open and wide (0); open and narrow (1).

Adriosaurus has been recoded from state 1 to ? as the interpterygoid vacuity cannot be observed.

69(119).**Pterygoid**- Anterior (palatine) process merges gradually, in a gentle curve, with the lateral (ectopterygoid) process (0); anterior process distinctly set off from lateral process, the two portions meeting at a distinct "corner" (1).

Adriosaurus has been recoded from state 1 to ? as the presence of the palatine process on specimen NHM R2867 is tentative.

(d) lower jaw

70(122).**Mandibular symphysis**- Rigid - anterior tips of dentary with a distinct flat symphysial area (0); mobile - anterior tips of dentary smoothly rounded and without distinct symphysial area (1).

71(123).**Mental foramina on lateral surface of dentary**- Three or more foramina (0); two or fewer foramina (1).

72(124).**Dentary**- Curved in lateral view, with concave dorsal (alveolar) edge (0); straight in lateral view, with straight dorsal edge (1).

73(125).**Dentary**- With small posterodorsal extension onto anterolateral part of coronoid process (0); does not cover lateral surface of coronoid process (1).

74(127).**Anterior** (symphysial) **end of Meckel's canal**- Extends along ventral margin of lower jaw (0); confined to medial surface of lower jaw (1).

75(129).**Subdental shelf**- Weakly developed (0); large (1); absent (2).

There is no evidence of a subdental shelf in Pachyrhachis (Lee and Caldwell, 1998), Pachyophis (Lee et al., 1999), and Serpentes; theses taxa have been recoded from - (not applicable) to state 2. On the other hand, aigialosaurs, mosasaurs (DeBraga and Carroll, 1993), and dolichosaurs (Caldwell, 1999) all have large subdental shelves and have been recoded from - (not applicable) to state 0.

76(130).**Posterior margin of lateral surface of dentary**- Shallow notch present (0); no notch present (1); deep notch present (2).

77(131).**Dentary-postdentary articulation**- Extensive overlap (0); reduced overlap (1).

78(132).**Splenial**- Large, extending anteriorly past middle of tooth row (0); small, only reaching middle of tooth row (1).

79(133).**Splenial**- Extends posteriorly onto postdentary bones, past apex of coronoid process (0); extends posteriorly onto postdentary bones but does not reach level of apex of coronoid process (1); does not substantially overlap postdentary elements (2).

80(134).**Anterior tip of Splenial**- On ventral edge of dentary (0); on medial surface of dentary (1).

81(135).**Splenial-dentary contact**- Extensive bony contact (0); reduced bony contact, much intervening connective tissue (1).

82(136).**Splenial-angular contact**- In medial view, overlapping, irregular, and with limited mobility (0); in medial view, abutting, straight (vertical), and highly mobile (1).

83(137).**Splenial-angular contact**- Not, or very slightly, exposed in lateral view (0); greatly exposed in lateral view (1).

84(138).**Anteromedial process of coronoid**- Long, extensive overlap on medial surface of dentary in front of coronoid process (0); short, coronoid does not greatly overlap medial surface of dentary in front of coronoid process (1).

85(139).**Anterolateral process of coronoid**- Present, overlapping lateral surface of dentary (0); absent, coronoid does not overlap lateral surface of dentary (1).

86(140).**Coronoid**- Anteromedial margin contacts splenial (0); anteromedial margin does not contact splenial (1).

87(141).**Coronoid**- Ventral margin of medial surface concave (0); ventral margin of medial surface straight or convex (1).

88(142).**Subcoronoid fenestra on medial surface of the mandible**- Fenestra present as distinct gap between coronoid and prearticular, surangular exposed in medial view (0); fenestra absent, prearticular expands dorsally

and contacts the entire ventral edge of the coronoid, surangular covered by these elements in medial view (1).

89(143).**Disarticulated surangular**- Extends far into the dentary and terminates in a point (0); extends some distance into the dentary and terminates in a blunt end (1); extends a short distance into the dentary and terminates in a blunt end (2); extends over lateral surface of dentary (3).

90(145).**Surangular**- Does not form large portion of articular cotyle (0); forms half of articular cotyle (1).

91(147).**Angular**- Not exposed, or exposed as only a very narrow splint, on the medial surface of the mandible (0); with wide exposure on medial surface of the mandible (1).

92(149).**Prearticular** (in medial view with dentary and splenial removed)- Extends well anterior to coronoid process, past posterior teeth (0); extends only a short distance in front of coronoid process, not past posterior teeth (1).

Pachyrhachis (1) and Serpentes (0&1) are recoded to - (not applicable) because neither has a definite prearticular (Lee and Caldwell, 1998).

93(151).**Adductor fossa**- Faces dorsomedially (0); faces dorsally (1).

94(153).**Articular**- Separate from both prearticular and surangular (0); fused with prearticular but not surangular (1); fused with prearticular and surangular (2).

95(154).**Retroarticular process size**- Intermediate, between 1 and 2 times

articular cotyle (0); short, < articular cotyle (1); long, >2 times articular cotyle (2).

96(156).**Retroarticular process orientation**- Extends posteromedially (0); extends straight posteriorly (1).

Pachyrhachis is recoded from - (not applicable) to ? because this character is not readily visible on the specimen (Lee and Caldwell, 1998).

97(159).**Retroarticular process**- Not tapering, broad distally (0); tapering, narrow distally (1).

Pachyrhachis is recoded from - (not applicable) to ? because this character is not readily visible on the specimen (Lee and Caldwell, 1998).

(e) dentition

98(161).**Marginal teeth**- Pleurodont, teeth set in a continuous groove (0); thecodont, teeth ankylosed in discrete alveoli and separated by well-developed interdental plates (1).

99(162).**Marginal teeth**- Without sharp carinae (0); with sharp carinae (1).

100(163).**Bases of marginal teeth**- Smooth, dentine not infolded (0); dentine infolded ("plicidentine"), resulting in longitudinal grooves (1).

Aigialosaurs and mosasaurs lack 'plicidentine' (Zaher and Riepel, 1999), but do display either infoldings of the enamal (Lingham-Soliar, 1994) or distinct ridges on the surface of the teeth; accordingly, aigialosaurs and mosasaurs have been recoded from state 1 to state 0. Pachyrhachis also lacks 'plicidentine' (per. obs.) and is recoded from state 1 to state 0.

101(164).**Marginal teeth**- Crowns closely spaced (0); crowns separated by large gaps (1).

102(165).**Marginal teeth**- Without high pedestals (0); with high pedestals (1).

103(167).**Resorption pits**- At base of teeth (0); on bony tooth pedicel (1); absent (2).

104(168).**Orientation of replacement teeth**- Erupt upright, growing straight upwards into functional position (0); erupt horizontally, and then rotating through ninety degrees about the base into functional position (1).

105(169).**Premaxillary teeth**- Five or more (0); four or fewer (1).

106(170).**Median premaxillary tooth**- Present (0); absent (1).

107(172).**Premaxillary teeth** (apart from median tooth)- Similar size or larger than anterior maxillary teeth (0); distinctly smaller than anterior maxillary teeth (1).

108(173).**Maxillary teeth**- Thirteen or more tooth positions (0); between twelve and nine tooth positions (1); eight or fewer tooth positions (2).

109(174).**Dentary teeth**- Thirteen or more tooth positions (0); twelve to nine tooth positions (1); eight or fewer tooth positions (2).

110(175).**Palatine teeth**- Absent (0); present (1).

111(176).**Palatine teeth**- Small conical denticles (0); similar in size to marginal teeth (1).

112(177).**Pterygoid teeth**- Present (0); absent (1).

113(178).**Pterygoid teeth**- Small conical denticles (0); similar in size to marginal teeth (1).

(f) axial skeleton

114(181).**Vertebral articulatory surfaces**- Slightly anterodorsal, condyles facing slightly dorsally, only the ventral edge of the articulatory surface is visible in ventral view (0); vertical, condyles (if present) facing posteriorly, much of the articulatory surface is visible in ventral view (1); anterodorsal, condyles facing very dorsally, none of the articulatory surface is visible in ventral view (2).

115(186).**Zygosphenes and zygantra**- Absent (0); present (1).

116(189).**Number of presacral vertebrae**- 27 to 50 (0); 50 to 119 (1); 23 to 25 (2); 120 or more(3).

117(190).**Number of cervical vertebrae**- Seven or fewer (0); eight (1); nine or ten (2); more than ten (3).

118(191).**Transverse processes of cervicals**.- On anterior end of centrum (0); on middle of centrum (1).

119(192).**Hypapophyses on anterior presacrals**- Only extending to the posterior end of the sixth presacral at most (0); extending to the seventh presacral or beyond (1).

120(194).**Cervical intercentra** (excluding atlas and axis intercentra)- Fused to preceding centrum (0); sutured to preceding centrum (1); not sutured or fused to preceding centrum (2).

121(196).**Pachyostosis of mid-dorsal vertebrae and ribs**- Absent (0); present (1).

122(202).**Pedestals on caudal vertebrae for chevrons**- Weakly developed,

barely raised above the surface of the centrum (0); prominent raised tubercles (1).

123(204).**Caudal chevron position**- At posteroventral margin of centrum (0); situated more anteriorly, some distance from posteroventral margin of centrum (1).

124(205).**Body shape**- Round, ribs smoothly curved (0); laterally compressed, middle and distal regions of ribs totally straight (1).

125(206).**Ribs**- Begin from third (or more anterior) cervical vertebra (0); begin from fourth (or more posterior) cervical vertebra (1).

126(209).**Distally forked cloacal ribs** ("lymphapophyses")- Absent (0); present (1).

127(210).**Tail**- Cylindrical or only slightly lateral compressed, transverse processes well-developed, chevrons and neural spines not elongated (0); very laterally compressed, transverse processes reduced anteriorly and absent posteriorly, chevrons and neural spines elongated (1).

128(211).**Neural spines of posterior caudal vertebrae**- Projecting dorsally or posterodorsally (0); projecting almost horizontally, highly inclined posteriorly (1).

(g) shoulder girdle and forelimb

129(212).**Scapulocoracoid**- Present and large (0); present but reduced (1); absent (2).

130(214).**Anterior** (primary) **coracoid emargination**- Present (0); absent (1).

131(216).**Clavicle**- Present (0); absent (1).

132(219).**Interclavicle**- Present (0); absent (1).

133(220).**Interclavicle**- Cross-shaped, with lateral processes (0); simple rod, without lateral processes (1).

134(222).**Ossified sternum**- Present (0); absent (1).

135(225).**Number of rib attachment points to sternum**- Four pairs (0); three pairs (1); five pairs (2); two pairs or fewer (3).

136(227).**Forelimbs**- Large (0); small (1), absent (2).

137(228).**Ectepicondylar foramen of humerus**- Present (0); absent (1).

138(229).**Epipodials**- Parallel (0); distally diverging (1).

139(230).**Forelimb**- "Foot" - olecranon large, carpals well-ossified, digits independently movable and with well-developed joints (0); "flipper" - olecranon small, carpals poorly-ossified, digits joined by webbing or sheath and with poorly-developed joints (1).

(h) pelvic girdle and hind limb

140(231).**Pelvis**.- Present and large (0); present and small (1); absent (2). Mosasaurs (Russell, 1967) display a reduce pelvic girdle and as such have been recoded from state 0 to state 1.

141(232).**Pelvic elements** (ilium, ischium, pubis)- Co-ossified into a single pelvic bone (0); distinct elements but strongly sutured together (1); distinct elements, weakly united in non-sutural contacts (2).

142(233).**Sacral blade of ilium**- With anterior bulge or process (0); without

anterior process (1).

143(235).**Pubic plate**- Oriented transversely, narrow in lateral view (0); oriented parasagitally, wide in lateral view (1).

144(236).**Pubis**- Expanded distally, at symphysial margin (0); not expanded distally (1).

145(237).**Hindlimbs**- Well-developed (0); reduced (1); absent (2).

146(238).**Femur**- Gracile (0); stout (1).

147(239).**Femur**- Curved in dorsoventral plane (0); not curved (1).

148(240).**Distal end of tibia**- With notch fitting into a ridge on astragalocalcaneum (0); gently convex for astragalocalcaneal articulation (1).

149(241).**Astragalus and calcaneum**- Coossified (0); separate (1).

150(242).**Hindlimb**- "Foot".- fifth metatarsal fully hooked, tarsals well-ossified, digits independently movable and with well-developed joints (0); "flipper" - fifth metatarsal partially hooked or not hooked, tarsals poorly-ossified, digits joined by webbing or sheath and with poorly-developed joints (1).

(i) miscellaneous osteological characters

151(243).**Body proportions**- Head moderately large with respect to trunk region (0); head extremely small with respect to trunk region (1).

152(244).**Dorsal body osteoderms**- Present (0); absent (1).

153(246).**Separable cranial osteoderms**- Present over entire skull table (0); absent (1).

154(248).**Separable cranial osteoderms**- Tightly connected to skull roof, though separable (0); very loosely connected to skull roof (1).

155(249).**Rugosities on skull roof bones formed by overlying cephalic scales**- Rugosities absent (0); rugosities present, no vermiculate sculpture (1); rugosities present, along with vermiculate sculpture (2).

156(250).**Scleral ossicles**- Present (0); absent (1).

157(251).**Scleral ossicles**- Fourteen (0); thirteen or fewer (1); fifteen or more (2).

158(255).**Epiphyses on skull and axial skeleton**- Present (0); absent (1).

159(256).**Epiphyses on appendicular skeleton**- Present (0); absent (1).

APPENDIX II

Data Matrix

Appendix 1.2 1		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
		2.	3.	4.	5.	8.	10.	11.	13.	15.	18.	19.	20.	21.	22.	24.
1	Anguidae	0	0	0	0	0	0	0	0	0	0	0	0&1	0	0	0
2	Xenosaurus	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0
3	Shinisaurus	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0
4	Heloderma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Lanthanotus	0	1	1	0	1	1	0	1	0	0	0	0	0	1	2
6	Varanus	0	1	1	0	1	1	0	1	0	0	0	0	0	1	2
7	Aigialosauridae	1	?	?	0	1	1	0	?	1	1	0	0	1	?	2
8	Mosasauridae	1	1	1	0	1	1	0	0	1	1	0	0	1	0	2
9	Dolichosauridae	?	?	?	0	1	1	?	?	?	?	?	?	0	?	?
10	Aphanizocnemus	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
11	Adriosaurus	?	?	?	1	1	0&1	0	?	0	?	?	?	?	?	?
12	Pachyrhachis	0	?	?	1	1	0	1	?	0	0	0	0	?	?	2
13	Pachyophis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Serpentes	0	1	0&1	1	0	0&1	1	0	0	-	-	0	0	0&1	1
15	Pontosaurus	?	?	0	0	1	1	?	?	1	0	1	0	1	0	2

Appendix 1.2 2		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
		26.	27.	28.	29.	31.	34.	35.	36.	37.	38.	42.	44.	46.	47.	48.
1	Anguidae	0	0&1	0&1	0	0	0	0	0	0	0	0	0&1	0	0	0
2	Xenosaurus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
3	Shinisaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
4	Heloderma	0	1	1	-	0	1	1	1	-	0	1	1	0	1	-
5	Lanthanotus	0	1	1	-	0	0	1	1	-	0	1	0	0	1	-
6	Varanus	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
7	Aigialosauridae	1	0	0&1	0	0&1	0	?	?	0	0	0	0	0	0	0
8	Mosasauridae	1	0	0	1	0&1	0	0&1	0	0	0	0	0	0	0	0
9	Dolichosauridae	?	0	0	0	0	?	1	?	?	?	?	?	?	?	?
10	Aphanizocnemus	?	0	0	0	?	0	?	?	?	?	0	1	?	?	?
11	Adriosaurus	0	1	0	0	0&1	0	1	?	1	?	0	0	?	0	?
12	Pachyrhachis	0	1	1	-	1	0	1	0	1	0	1	2	1	1	-
13	Pachyophis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Serpentes	0	1	0&1	0&1	1	1	1	0&1	1	1&2	1	2	1	1	-
15	Pontosaurus	1	0	0	1	0	0	1	0	1	?	0	2	0	0	0

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		31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
		51.	55.	56.	57.	58.	59.	61.	63.	64.	67.	69.	71.	72.	73.	74.
1	Anguidae	0	0	0	0	0	0	0&1	0	0	0	0&1	0&1	0	0	0
2	Xenosaurus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Shinisaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Heloderma	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
5	Lanthanotus	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
6	Varanus	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0
7	Aigialosauridae	0	0	?	1	?	?	0	1	1	?	?	?	?	0	1
8	Mosasauridae	1	0	1	1	1	1	0	1	1	0	1	1	0	0	1
9	Dolichosauridae	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
10	Aphanizocnemus	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11	Adriosaurus	?	1	?	1	?	?	?	?	?	?	1	?	?	?	?
12	Pachyrhachis	0	1	1	1	1	1	2	0	?	?	1	1	1	1	1
13	Pachyophis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Serpentes	-	1	1	0&1	1	1&2	0&2	0	0&1	2	1	1	1	1	1
15	Pontosaurus	0	1	?	0	?	?	0	1	1	?	0	?	?	?	?

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		46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
		75.	78.	80.	85.	86.	87.	88.	89.	90.	91.	92.	95.	96.	98.	100
1	Anguidae	0	0&1	0	0&1	0	0	0	0&1	0	0	0	0	0	0	0
2	Xenosaurus	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0
3	Shinisaurus	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0
4	Heloderma	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0
5	Lanthanotus	0	1	1	?	0	1	0	0	1	1	0	0	0	0	0
6	Varanus	0	0	1	1	0	1	1	0	1	1	0	0	0	0	0
7	Aigialosauridae	?	?	?	?	1	1	?	?	?	?	?	0	?	?	?
8	Mosasauridae	0	0	1	1	1	1	1	1	0	2	0	0	1	1	1
9	Dolichosauridae	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
10	Aphanizocnemus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11	Adriosaurus	?	?	?	?	?	?	?	?	?	2	?	?	?	?	?
12	Pachyrhachis	1	?	?	?	1	?	?	?	?	2	1	1	1	?	2
13	Pachyophis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Serpentes	1	1	1	0	1	1	1	1	0	2	1	1	1	1	2
15	Pontosaurus	?	?	?	0	1	1	?	?	?	2	1	?	?	?	?

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		61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
		104	105	108	109	111	113	114	116	119	122	123	124	125	127	129
1	Anguidae	0	0	0	0	0	0	0&1	0	0	0	0	0	0&1	0	0
2	Xenosaurus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
3	Shinisaurus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
4	Heloderma	1	0	0	1	0	0	1	0	0	0	0	0	1	0	2
5	Lanthanotus	0	0	0	1	0	0	1	0	0	0	0	0	1	0	2
6	Varanus	1	0	0	1	0	0	1	0	0	0	0	0	1	0	2
7	Aigialosauridae	?	?	?	?	?	0	?	?	?	1	0	1	1	1	1
8	Mosasauridae	1	0	0	1	0	0	0	1	1	1	0	1	1	1	1
9	Dolichosauridae	?	?	?	?	?	?	?	?	?	?	0	1	1	1	1
10	Aphanizocnemus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11	Adriosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12	Pachyrhachis	?	1	1	0	1	0	0	0	?	1	1	1	1	1	2
13	Pachyophis	?	?	?	?	?	?	?	?	?	1	?	1	1	1	2
14	Serpentes	0&1	1	1	0&1	1	-	0	0	1	1	1	0&1	1	1	2
15	Pontosaurus	?	?	?	?	?	?	0	1	0	1	1	1	1	1	0

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		76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
		130	131	132	133	134	135	136	137	138	139	140	141	142	143	145
1	Anguidae	0	0	0&1	0	0	0	0	0	0	0	0	0	0	0	0
2	Xenosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Shinisaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Heloderma	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0
5	Lanthanotus	0	1	1	2	0	1	0	0	1	1	0	0	0	2	0
6	Varanus	0	1	0	1	0	1	0	0	0	1	0	0	0	2	0
7	Aigialosauridae	1	1	0	2	1	?	1	1	1	1	?	1	1	2	1
8	Mosasauridae	1	1	0	2	1	1	1	1	1	1	1	1	1	2	1
9	Dolichosauridae	1	?	?	2	1	?	1	?	0	0	0	1	1	?	?
10	Aphanizocnemus	?	?	0	?	?	?	1	?	?	?	?	?	?	?	?
11	Adriosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
12	Pachyrhachis	2	1	0	2	1	1	1	?	0	1	1	1	1	3	-
13	Pachyophis	?	1	?	?	?	?	1	1	?	?	?	?	?	3	?
14	Serpentes	2	1	1	2	1	1	1	0&1	1	1	1	1	1	3	-
15	Pontosaurus	1	1	1	2	1	1	1	1	1	1	0	1	1	?	0

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		91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
		147	149	151	153	154	156	159	161	162	163	164	165	167	168	169
1	Anguidae	0	0	0	0	0	0	0	0	0	0&1	0	0	0	0	0
2	Xenosaurus	0	0	0	0	2	1	1	0	0	0	0	0	0	0	0
3	Shinisaurus	0	0	0	0	2	1	1	0	0	0	0	0	0	0	0
4	Heloderma	1	0	0	0	0	0	1	0	1	1	1	0	2	0	0
5	Lanthanotus	1	1	0	0	0	0	1	0	1	1	1	0	2	0	0
6	Varanus	1	1	0	0	0	0	1	0	1	1	1	0	2	0	0
7	Aigialosauridae	1	0	1	1	0	0	0	1	1	0	1	1	2	?	1
8	Mosasauridae	1	0	1	1	0	0	0	1	1	0	1	1	1	1	1
9	Dolichosauridae	1	?	?	?	?	?	?	1	0	0	-	0	2	1	?
10	Aphanizocnemus	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?
11	Adriosaurus	?	?	?	?	0	0	0	?	?	?	1	0	?	?	1
12	Pachyrhachis	1	-	1	2	1	?	?	1	1	0	1	0	2	?	1
13	Pachyophis	?	?	?	?	?	?	?	1	?	?	1	0	?	?	?
14	Serpentes	1	-	1	2	&1&	0	1	1	1	0&1	1	0	2	1	1
15	Pontosaurus	1	0	0	1	2	0	0	?	1	0	?	?	?	?	?

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		106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
		170	172	173	174	175	176	177	178	181	186	189	190	191	192	194
1	Anguidae	0	0	0	0	0	0	0&1	0	0	0	0&1	0&1	0	0&1	0
2	Xenosaurus	0	0	0	0	0	-	1	0	0	0	0	0	0	0	0
3	Shinisaurus	0	0	0	0	0	-	0	0	0	0	2	0	0	0	0
4	Heloderma	0	1	1	1	0&1	0	0	0	0	0	0	0	0	0	0&1
5	Lanthanotus	0	1	1	1	1	0	0	0	2	0	0	2	0	1	0&1
6	Varanus	0	1	1	1	0	-	1	-	2	0	0	2	0	1	0
7	Aigialosauridae	?	?	0	0	?	?	?	?	0	1	0	2	1	1	2
8	Mosasauridae	1	1	0	0	0	-	0	1	0&1	1	0	2	1	1	2
9	Dolichosauridae	?	?	0	0	?	?	?	?	0	1	&1&	3	0	1	0
10	Aphanizocnemus	?	?	?	?	?	?	?	?	?	1	0	3	0	1	2
11	Adriosaurus	?	1	0&1	?	?	?	?	?	0	1	0	3	0	?	?
12	Pachyrhachis	?	?	0	0	1	1	0	1	1	1	3	3	0	1	0
13	Pachyophis	?	?	?	0	?	?	?	?	?	1	3	3	0	?	?
14	Serpentes	1	1	&1&	&1&	0&1	1	0&1	1	0&1	1	3	-	0	0&1	0
15	Pontosaurus	?	?	0	0	0	-	1	-	?	?	0	3	0	1	1

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		121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
		196	202	204	205	206	209	210	211	212	214	216	219	220	222	225
1	Anguidae	0	0	0	0	0&1	0	0	0	0&1	0	0	0&1	0	0	0&1
2	Xenosaurus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
3	Shinisaurus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
4	Heloderma	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0
5	Lanthanotus	0	1	1	0	1	0	0	0	0	0	0	0	0	0	3
6	Varanus	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1
7	Aigialosauridae	0	1	1	0	0	0	1	1	0	1	0	0	0	0	2
8	Mosasauridae	0	1	1	0	0	0	1	1	0	0&1	0	0	1	0	2
9	Dolichosauridae	0	?	1	0	?	0	?	?	1	1	?	1	?	0	?
10	Aphanizocnemus	0	1	1	0&1	?	0	1	1	1	0	0	?	?	?	?
11	Adriosaurus	1	1	1	1	?	0	1	1	1	?	?	?	?	?	?
12	Pachyrhachis	1	?	?	1	?	1	1	?	2	-	1	1	-	1	-
13	Pachyophis	1	?	?	1	?	?	1	?	2	-	1	1	-	1	-
14	Serpentes	0	-	1	0	0	1	0	-	2	-	1	1	-	1	-
15	Pontosaurus	1	?	?	1	0	?	?	?	1	1	?	0	?	1	?

Appendix 1.2 10

		136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
		227	228	229	230	231	232	233	235	236	237	238	239	240	241	242
1	Anguidae	&1&	0	0	0	0&1	0	0&1	0	0	0&1	0	0	0	0	0
2	Xenosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Shinisaurus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
4	Heloderma	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
5	Lanthanotus	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
6	Varanus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
7	Aigialosauridae	0	1	1	1	0	2	1	1	0	0	1	1	1	1	1
8	Mosasauridae	0	1	1	1	1	2	1	1	0	0	1	1	1	1	1
9	Dolichosauridae	1	?	?	?	1	?	?	?	?	1	1	1	?	?	?
10	Aphanizocnemus	1	1	?	1	1	2	1	1	1	1	1	?	?	1	1
11	Adriosaurus	1	1	1	1	1	2	1	1	1	1	1	?	?	1	1
12	Pachyrhachis	2	-	0	-	1	2	1	1	1	1	1	1	1	1	1
13	Pachyophis	2	-	?	-	?	?	?	?	?	?	?	?	?	?	?
14	Serpentes	2	-	-	-	1&2	2	1	-	-	1&2	-	-	-	-	-
15	Pontosaurus	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?

Appendix 1.2 11

		151	152	153	154	155	156	157	158	159
		243	244	246	248	249	250	251	255	256
1	Anguidae	0	0	0	0	0&1	0	0&1	0	0
2	Xenosaurus	0	0	0	0	2	0	0	0	0
3	Shinisaurus	0	0	0	0	2	0	0	0	0
4	Heloderma	0	0	0	0	1	0	1	0	0
5	Lanthanotus	0	0	0	1	0	0	1	0	0
6	Varanus	0	0&1	0&1	1	0&1	0	2	0	0
7	Aigialosauridae	0	1	1	-	0	?	?	1	0
8	Mosasauridae	0	1	1	-	0	0	0	1	1
9	Dolichosauridae	0	1	1	?	0	?	?	?	0
10	Aphanizocnemus	0	1	1	-	0	?	?	?	?
11	Adriosaurus	0	1	1	-	0	?	?	?	0
12	Pachyrhachis	1	1	1	-	0	1	-	1	1
13	Pachyophis	1	1	?	?	?	?	?	?	?
14	Serpentes	0	1	1	-	0	1	-	1	1
15	Pontosaurus	1	1	1	-	0	?	?	?	0

CHAPTER TWO

EVALUATION OF DOLICHOSAUR INTERRELATIONSHIPS

INTRODUCTION

Dolichosaurs have recently been highlighted as an important source of information in the debate on the origins and evolution of snakes. However, our current understanding of the interrelationships of dolichosaurs and their phylogenetic position among squamates continues to remain highly tentative. Preliminary cladistic results indicate that dolichosaurs are a non-monophyletic assemblage nested within the Pythonomorpha (mosasauroids and snakes) as the sister-group to snakes (Lee and Caldwell, 2000; Pierce and Caldwell, 2002). The current research is designed to addresses dolichosaur interrelationships in order to expand our knowledge of this enigmatic group and to contribute new information towards a resolution of snake origins.

Snake Origins and Evolution

Cope (1869) was the first author to examine the evolutionary relationships of three groups of squamates, snakes, varanids, and mosasaurs, all of which are central to the problem of dolichosaur phylogeny. He considered mosasaurs–giant, extinct, marine lizards–to be the nearest relatives to snakes and referred to the mosasaur-snake clade as the Pythonomorpha. Cope's position on snake relationships proved highly controversial and provoked the beginning of an intensive debate in the late 1800's. Although some researchers (Boulenger, 1891; Osborn, 1899) recognized merit in Cope's (1869; 1878; 1895a, b; 1896a, b) proposal, others (Owen, 1877, 1878; Baur, 1895, 1896) criticized his hypothesis by emphasizing that mosasaurs where derived, aquatic varanoid lizards without any relationship to snakes.

By the early 20th century the snake controversy had expanded to include several new evolutionary hypotheses. One was an extension of Cope's (1869) idea asserting that snakes were most closely related to dolichosaurs and secondarily related to mosasaurs and aigialosaurs (Nopsca, 1908; 1923); dolichosaurs were never considered by Cope because Owen (1850) had misidentified them as marine 'iguanian' lizards with no affinities to snakes, varanids, or mosasaurs. A second suggested that snakes had descended from terrestrial lizard-like animals living in areas of dense vegetation or burrowing beneath the surface (Janensch, 1906; Camp, 1923; Radovanovic, 1935). Finally, a third stated that neither fossil varanoids nor any extant lizard group could serve as plausible snake ancestors and that snakes had evolved from an earlier form of reptile (Fejérvary, 1918).

Ever since these early works, successive generations of systematists have continued to examine the origin and evolution of snakes (Brock, 1941; McDowell and Bogert, 1954; Hoffstetter, 1955; Underwood, 1957a, b, 1970; McDowell, 1972; Senn and Northcutt, 1973; Kochva, 1978; Rieppel, 1977, 1978; 1983, 1988; Rage 1982; Evans, 1984); however, evidence used to infer evolutionary relationships was based purely on conjecture. Estes et al. (1988) were the first to conduct a modern cladistic analysis in order to evaluate the phylogenetic relationships of squamates. The study included all known modern squamate groups including snakes. Unfortunately, the analysis could only conclude that snakes were 'Scleroglossa inserta sedis', i.e. snakes belonged somewhere within a large clade composed of all squamates except iguanians. Thus, even with the use of modern statistical programs the interrelationships of snakes remained uncertain.

A decade after Estes et al.'s (1988) innovative study, Lee (1997) examined the sister group relationships of snakes in a more exclusive cladistic study that integrated both modern and fossil taxa. He added modern snakes to an analysis of the Platynota, the clade consisting of living varanoids (i.e., Varanus) and their fossil representatives (i.e., mosasaurs). Evidence indicated that extinct mosasauroids (aigialosaurs and mosasaurs) were the nearest relatives of snakes; as a result, the name Pythonomorpha was reinstated to describe the mosasauroid-snake clade. This study not only substantiated Cope's (1869) original hypothesis, but also demonstrated how important fossil taxa are in the resolution of evolutionary relationships.

Modern resolution of snake origins stimulated the re-examination of the Cretaceous fossil squamate Pachyrhachis problematicus. Haas (1979; 1980a, b) originally described Pachyrhachis as a lizard showing a curious mixture of varanoid and snake characters (a dolichosaur-like animal); however, he was unsure if the animal was directly related to snakes–and thus intermediate between varanoid lizards and snakes–or merely convergently snake-like. Reanalysis of the fossil material by Caldwell and Lee (1997) and Lee and Caldwell (1998) established Pachyrhachis to be a marine snake with a functional pelvis and hind limb. A phylogenetic analysis found Pachyrhachis to be the sister-group to all modern snakes and the Pachyrhachis-snake clade to be closely related to mosasauroids (mosasaurs and aigialosaurs). Thus Pachyrhachis is considered to be a basal snake and snakes appear to have originated from marine lizards (see also Lee, 1998; Caldwell, 1999a; Cohn and Tickle, 1999; Lee and Caldwell, 2000; Lee and Scanlon, 2002).

The interpretation of Pachyrhachis as a 'missing link' between aquatic reptiles and terrestrial snakes has been challenged repeatedly. Zaher (1998) and Zaher and Rieppel (1999) reviewed the anatomy of Pachyrhachis and modified a number of characters with respect to its recent redescription (Caldwell and Lee, 1997; Lee and Caldwell, 1998). A constrained phylogenetic analysis found Pachyrhachis to be within the clade Serpentes (all modern snakes) as the sister group to advanced (macrostomatan) snakes and not a basal snake. Considering these new findings Rieppel and Zaher (2000) added their reinterpretation of Pachyrhachis to a revised version of Lee's (1998) global squamate data set that supported the basal position of Pachyrhachis among snakes. The analysis produced a tree in which snakes formed a clade with a monophyletic group comprising amphisbaenians and dibamids (burrowing lizards). Thus Pachyrhachis is considered to be a derived snake and snakes appear to have originated from fossorial lizards (see also Zaher and Rieppel, 2000).

Since the exhaustive analysis of Pachyrhachis, two new fossil marine snakes with hind limbs (Haasiophis, Eupodophis) and one fossil terrestrial snake (Dinilysia) have been discussed in detail in the literature (Tchernov et al., 2000; Rage and Escuillié, 2000; Lee and Scanlon, 2002); however, all appear to display the same degree of phylogenetic plasticity as Pachyrhachis. In other words, the origin (marine vs. burrowing) and interrelationships of fossil (primitive vs. derived) and modern snakes is highly dependant on how one interprets the anatomy of fossil snakes and on which data matrices snakes are included in. Therefore, to better elucidate the affinities of snakes, a group of small Cretaceous marine lizards known as dolichosaurs have recently been re-examined in terms of anatomy and phylogeny. Nopcsa (1908; 1923) at the beginning of the 20th

century had highlighted dolichosaurs as the possible sister-group to snakes, although, until now the existing descriptions of dolichosaur anatomy were too old, brief, and inaccurate to incorporate into a cladistic analysis.

Dolichosaur Interrelationships

Kramberger (1892) was the first author to examine dolichosaurs in terms of morphology and phylogeny. He analyzed and compared known marine lizards from the Adriatic coast and England and separated them into two families. The first family, the Aigialosauridae, included all the Adriatic lizards Pontosaurus, Adriosaurus, Acteosaurus, and Aigialosaurus; the second family, the Dolichosauridae, included the English lizard Dolichosaurus. Both families where grouped together into a larger assemblage, the 'Ophiosauria'. Kramberger (1892) considered the 'Ophiosauria', and by extension dolichosaurs, to be a transitional group between the 'lizards' and mosasaurs.

Soon after Kramberger's (1892) study, Nopcsa (1903) conducted a detailed examination of the anatomy of both dolichosaurs and aigialosaurs and compared them to varanids and mosasaurs. Nopcsa (1903) acknowledged two sharply separated groups of lizards. The first was the long-necked, small-headed dolichosaurs and the second was the short-necked and large-headed aigialosaurs. Based on this distinction, Nopcsa (1903) restructured Kramberger's (1892) classification system. Pontosaurus, Acteosaurus, and Adriosaurus were removed from the Aigialosauridae and added to the Dolichosauridae based on similarities between Dolichosaurus and these Adriatic lizards. Nopcsa (1903) also concluded that mosasaurs had descended from aigialosaurs and both shared a common ancestry with varanids. The relationships of dolichosaurs, although

acknowledged to represent a distinct family of 'lizard', remained unclear with regard to descent.

Nopcsa (1908; 1923) tried to resolve the systematic position of dolichosaurs in another more comprehensive study that included a comparison with snakes. He explained that dolichosaurs showed genealogical relationships to anguids, varanids, aigialosaurids, and mosasaurids, but seemed to be most closely related to snakes. In fact, Nopcsa (1908) stated: '...dolichosaurs are those which, through the smallness of the skull, increase in the number of cervical vertebrae, thoroughly snake-like zygosphenal articulations, cylindrical body and reduction of the extremities, show the strongest tendency to develop snake-like ways and hence, evidently, are genetically closest to these animals'. Nopcsa's (1908, 1923) claim of a close evolutionary relationship between dolichosaurs and snakes reinforced Cope's (1869) controversial hypothesis that snakes had evolved from marine reptiles.

Since Nopcsa (1923), dolichosaurs have remained unexamined; however, over the past several years, four previously identified dolichosaur species and two new taxa have been described in detail in the literature. Modern resolution of dolichosaur affinities began with the description of a new species of aquatic lizard from the Cretaceous of Lebanon, Aphanizocnemus libanensis (Dal Sasso and Pinna, 1997). Relationships of this dolichosaur were analyzed within a cladogram of the Varanoidea, including varanids, aigialosaurs, and mosasaurs. Aphanizocnemus occupied a transitional position with aigialosaurs between terrestrial varanids and fully aquatic mosasaurs, a scenario that supported Kramberger's (1982) 'Ophiosauria' hypothesis.

Caldwell and Cooper (1999) initiated the re-assessment of previously known dolichosaurs in an effort to diagnose their anatomy and elucidate their phylogenetic history. They re-described the dolichosaur Coniasaurus crassidens, but no phylogenetic analysis was conducted. Subsequently, Caldwell (1999a) described a new species of coniasaur, C. gracilodens, and added the anatomical characteristics of both coniasaur species to a phylogenetic analysis that included aigialosaurs and mosasaurs. The results found Coniasaurus to be the sister taxon to mosasauroids. The phylogenetic conclusion reached by Caldwell (1999a) was substantiated by Caldwell (2000) when the re-description of Dolichosaurus was added to the same analysis. Dolichosaurus was found as the sister taxon to Coniasaurus, with Coniasaurus being the sister taxon to mosasauroids. Again these results supported Kramberger's (1982) 'Ophiosauria' hypothesis.

To gain a better understanding of dolichosaur relationships and to test Nopcsa' s (1908; 1923) claim of a close evolutionary relationship between dolichosaurs and snakes, Caldwell (1999b) added Coniasaurus to a phylogenetic study of global squamate relationships. The cladistic analysis found Coniasaurus to be the sister-group to the Mosasauroidea. In turn, the clade Coniasaurus-Mosasauroidea was the sister-group to snakes. This analysis supported Lee's (1997) conclusions of a close evolutionary relationship between mosasauroids and snakes, a group he referred to as the Pythonomorpha; however, the analysis did not substantiate Nopcsa's (1908, 1923) claim of a closer evolutionary relationship between dolichosaurs and snakes to the exclusion of mosasauroids.

Two recent and complementary studies on dolichosaur relationships have recovered a dolichosaur-snake association. Lee and Caldwell (2000) re-described the dolichosaur Adriosaurus suessi and added it to a global squamate phylogenetic analysis along with all other proposed pythonomorphs: modern snakes, pachyophiids (Pachyrhachis and Pachyophis), mosasaurids, aigialosaurids, and all currently described or re-described dolichosaurs including Aphanizocnemus, Dolichosaurus, and Coniasaurus. The cladistic analysis recovered a cladogram that illustrated dolichosaurs to be a non-monophyletic group that formed successive sister taxa to snakes. Adriosaurus was resolved as the closest sister taxon to the Ophidia, a clade containing both fossil and modern snakes. The Dolichosauridae, which in this analysis combined the osteological features of Dolichosaurus and Coniasaurus into one terminal taxon, and Aphanizocnemus, formed an unresolved dichotomy that was the sister group to the Adriosaurus-snake clade. Further inclusion of the re-described dolichosaur Pontosaurus lesinensis into the same analysis by Pierce and Caldwell (2002) supported the topological relationships established by Lee and Caldwell (2000), with Pontosaurus nesting within the cladogram as the sister taxon to the Adriosaurus-snake clade.

Objectives

The current study is designed to examine dolichosaur relationships more closely through performing a more exclusive phylogenetic analysis. More specifically, the resolution of dolichosaur affinities will be assessed by examining the interrelationships of the Pythonomorpha. Lee (1997) was the first to perform a comprehensive cladistic analysis of the Pythonomorpha (varanids, mosasauroid, and snakes). Unfortunately, both

dolichosaurs and fossil snakes, which Lee (1997) agreed should be incorporated into the ingroup, were omitted because existing descriptions were old, very brief and inaccurate in many respects. Now, with the re-description of six dolichosaur species and three relatively complete fossil snakes, both dolichosaurs and fossil snakes can be integrated into an analysis of the Pythonomorpha. Results of this study will assist in determining whether the family Dolichosauridae is monophyletic and whether dolichosaurs are more closely related to snakes than to other marine squamates (mosasauroids).

MATERIALS AND METHODS

Matrix Structure and Analysis

A taxon-character matrix was compiled using 17 terminal taxa and 80 osteological characters (Appendices I and II). A series of 5 separate tests (i.e., taxonomic jackknifing) of the taxon-character matrix were conducted by excluding various taxa and characters from the analysis. Each taxon-character set was analyzed using the Branch-and-Bound algorithm in the software program PAUP Version 4.0b10 (Swofford, 2002). All multistate characters were left unordered and all multistate taxa were interpreted as polymorphic. A bootstrap analysis (1000 replicates) was conducted to assess the relative support values for resolved clades in the primary tree. The distribution of characters on the shortest tree was mapped using the accelerated transformation (ACCTRAN) character state optimization. The effect is that changes appear lower in the tree, thereby identifying synapomorphies (unequivocal and equivocal) for more inclusive clades, rather than being

optimized as apomorphies of more exclusive clades or even terminal taxa (DELTRAN) (Swofford, 2002).

Character Selection

The characters described (Appendix I) and coded in the data matrix (Appendix II) were selected from relatively recent studies that examined some aspect of pythonomorph relationships: Carroll and deBraga (1992); deBraga and Carroll (1993); Caldwell et al. (1995); Caldwell (1996); Lee (1997); Caldwell (1999a); Caldwell (1999b); Caldwell (2000); Lee and Caldwell (2000; an extension of Lee, 1998); and Lee and Scanlon (2002). It must be noted, however, that many of the characters discussed in these papers originated from earlier studies on squamate relationships. Taking into account all the data from the aforementioned studies, a list of over 800 osteological characters was assembled. Ultimately, only characters that could be coded for at least one dolichosaur terminal taxon were utilised; therefore, after eliminating all uninformative and redundant characters, a list composed of only 76 characters remained. Furthermore, during my own examination of the taxa included in this study, 14 of the 76 characters were modified with respect to dolichosaur anatomy and 4 new characters were created.

Outgroup

The extant lepidosaur Varanus was used as the outgroup in this analysis for rooting the tree and establishing character polarities. Varanus was selected as the outgroup because the majority of recent studies find varanoids to be the closest sister group to pythonomorphs (Lee, 1997; Lee, 1998; Lee and Caldwell, 2000; Pierce and

Caldwell, 2002). The Varanoidea are composed of three extant genera including Varanus, Lanthanotus, and Heloderma, plus a variety of fossil taxa. Out of all the varanoid taxa described, however, Varanus is the best known. Furthermore, unlike Lanthanotus and the fossil taxa, Varanus material is easily accessible; additionally, as compared to Heloderma, a layer of scales does not mask the skull in Varanus.

Ingroup

Ascertaining dolichosaur interrelationships is the principal theme of the analysis presented here. As such, the most current phylogenetic hypothesis on dolichosaur relationships (Pierce and Caldwell, 2002) was used to establish the composition of the ingroup. Dolichosaurs are part of the Pythonomorpha, a clade that has been defined as including the most recent common ancestor of mosasauroids and snakes, and all its descendants (Lee, 1997; 1998). Therefore, the ingroup in this study is composed of 16 taxa from the clade Pythonomorpha including mosasaurs, aigialosaurs, dolichosaurs and snakes (Appendix II).

A few differences exist between the ingroup composition of this study and that conducted by Pierce and Caldwell (2002). First, only the Pythonomorpha are examined here; therefore, all other squamate clades have been excluded. Second, several additional dolichosaur taxa have been added to the ingroup, including Acteosaurus, Eidolosaurus, and an undescribed specimen MSNM V3662; additionally, Dolichosaurus and both species of Coniasaurus are separate terminal taxa. Third, the poorly preserved fossil snake Pachyophis has been replaced by the fully articulated fossil snakes Haasiophis and Dinilysia. And fourth, the crown group Serpentes has been separated into two terminal

taxa, the Scolecophidia and Alethinophidia; this will give fossil snakes a chance to position within the clade Serpentes during the analysis.

Specimen List

Examination of the following specimens and/or published descriptions was used to development the characters, character states, and codings: Varanus: V. rudicollis CNHM 145710, Varanus UAMZ 385, Varanus UAMZ 391, and Bahl (1938); Pontosaurus: holotype GBA 1873/4/2 and Pierce and Caldwell (2002); Adriosaurus: Lee and Caldwell (2000) and Lee and Caldwell (2002); Aphanizocnemus: colour photographs of holotype MSNM V783 and Dal Sasso and Pinna (1997); Dolichosaurus: Caldwell (2000); Coniasaurus crassidens: Caldwell and Cooper (1999); Coniasaurus gracilodens: Caldwell (1999a); Acteosaurus: cast of holotype MCSNT 9960 and Meyer (1860); Eidolosaurus: cast of holotype GBA 1923/1 and Nopcsa (1923); MSNM V3662: colour photographs and Dal Sasso and Renesto (1999); Aigialosauridae: Carroll and deBraga (1992), deBraga and Carroll (1993), Caldwell et al. (1995), and Polcyn et al. (1999); Mosasauridae: Platecarpus UALVP unnumbered, Russell (1967), and deBraga and Carroll (1993); Pachyrhachis: Lee and Caldwell (1998), Zaher and Rieppel (1999), and Rieppel and Zaher (2000); Haasiophis: Tchernov et al. (2000); Dinilysia: Estes et al (1970), Hecht (1982), and Caldwell and Albino (2002); Scolecophidia: Typhlops punctatus USNM 320704, Rieppel (1979), and Lee (2002); Alethinophidia: Python UAMZ 383, Python WIP 1899, Xenopeltis unicolor USNM 287277, Lexocemus bicolour USNM 348509, Cylindrophis rufus USNM 297456, Rieppel (1977), Rieppel (1979), Rieppel (1983), Lee (2002), and Dr. Gavin Hanke's personal collection including:

Eunectes murinus, Corallus caninus, Corallus enydris cooki, Python regius, Boiga dendrophila, Psammophis sibilans subtaeniatus, Oxybelis aeneus auratus, Crotalus horridus atricaudatus, Sistrurus catenatus catenatus, Lampropeltis triangulum sinaloae, Thamnophis sirtalis parietalis, and Elaphe helena.

Institutional Abbreviations

CNHM, Chicago Natural History Museum, Chicago, Illinois; GBA, Austrian Geological Survey, Wien, Austria; MCSNT, Museo Civico di Storia Naturale di Trieste, Trieste, Italy; MSNM, Museo di Storia Naturale di Milano, Milan, Italy; UAMZ, University of Alberta Museum of Zoology, Alberta, Canada; USNM, National Museum of Natural History, Washington, D.C.; WIP, The Wistar Institute, Philadelphia, Pennsylvania.

PHYLOGENETIC RESULTS AND DISCUSSION

The following section is organized into a series of 5 tests: Test 1 includes all taxa and characters; Test 2 excludes all fossil and modern snakes; Test 3 excludes all fossil snakes; Test 4 excludes mosasauroids; and Test 5 excludes character 67 or pachyostosis. Each test is examined separately in terms of results and discussion.

Test 1: All taxa and characters included

Results—A Branch-and-Bound search of all 17 taxa and 80 characters resulted in 3 shortest cladograms (152 steps) with a Consistency Index (C.I.) of 0.72 and a Retention Index (R.I.) of 0.80. The only difference between the 3 trees recovered was the

relationships among Dolichosaurus longicollis, Coniasaurus crassidens, and Coniasaurus gracilodens. The same tree topology was recovered in both the strict consensus tree and the 50% majority-rule consensus tree (Fig. 2-1). The Mosasauridae and Aigialosauridae form a robust clade and appear as the sister group to dolichosaurs and snakes. Almost all remaining taxa form successive sister taxa to the clade containing scolecophidian and alethinophidian snakes. D. longicollis, C. crassidens, and C. gracilodens comprise an unresolved, but relatively well-supported clade. Pontosaurus and Eidolosaurus also form a clade, however, evidence for this relationship is weak. MSNM V3662 appears as a new species of dolichosaur and Adriosaurus is recovered as the closest sister taxon to fossil and modern snakes. Additionally, all three fossil snakes fall outside the modern snake clade with Pachyrhachis being the most basal snake.

The cladogram recovered from Test 1 illustrates a series of more exclusive clades ascending the tree from the Pythonomorpha to Serpentes (Fig. 2-1). All new clades that were produced by incorporating dolichosaurs into an analysis of the Pythonomorpha are here identified by a letter (A through I) and not given formal taxonomic names. The following is a synapomorphy list for each recovered clade. Numbers in brackets refer to the character number, the consistency index, and the state change. Single arrows designate equivocal characters, while double arrows designate unequivocal characters.

Mosasauroidea: Mosasauridae and Aigialosauridae.

Premaxilla contacts frontal (1, 0.5, 0→1), nasals reduced or absent (3, 1.0, 0⇒1), septomaxilla-maxilla contact mobile (6, 0.5, 0→1), prefrontal with antorbital ridge (12, 1.0, 0⇒1), frontals fused (13, 0.5, 0→1), frontal with sagittal crest (17, 0.5, 0→1),

descensus parietalis prominent flanges not contacting basisphenoid (20, 1.0, 0→1), parietal narrow posteriorly or triangular (22, 1.0, 0⇒1), supratemporal in deep position on ventrolateral surface of parietal (26, 1.0, 0⇒1), jugal extends anteriorly past orbit (34, 1.0, 0⇒1), quadrate circular in lateral view (36, 0.5, 0→1), quadrate tympanic crest directed laterally and a well-developed wall (37, 1.0, 0→1), basal tubera long (38, 0.5, 0→1), posterior border of opening for jacobson's organ not enclosed by bone (42, 1.0, 0→1), splenial-angular contact greatly exposed in lateral view (48, 0.5, 0→1), splenial not sutured to coronoid, but bones in contact (49, 0.5, 0→1), surangular enters and forms half of the articular cotyle (50, 0.667, 0→1), articular fused with prearticular, but not surangular (52, 1.0, 0→1), retroarticular process with medial flange (53, 0.5, 0→1), pterygoid toothed (56, 0.333, 0→1), tooth pedestals present (57, 0.5, 0⇒1), ribs begin from third vertebrae (61, 0.5, 0⇒1), caudal transverse processes absent on distal caudal vertebrae (69, 0.5, 0→1), caudal neural spines taller than dorsal neural spines, tail dorsoventrally expanded (70, 0.5, 0→1).

Clade A: Dolichosauridae, Aphanizocnemus, Acteosaurus, Eidolosaurus, Pontosaurus, MSNM V3662, Adriosaurus, and Ophidia.

Septomaxilla-maxilla contact mobile (6, 0.5, 0→1), frontals fused (13, 0.5, 0→1), frontal with sagittal crest (17, 0.5, 0→1), posterior border of opening of jacobson's organ not enclosed by bone (42, 1.0, 0→1), splenial-angular contact greatly exposed in lateral view (48, 0.5, 0→1), splenial not sutured to coronoid, but bones in contact (49, 0.5, 0→1), pterygoid toothed (56, 0.333, 0→1), caudal transverse processes absent on distal

CANADIAN THESIS
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REDESCRIPTION OF PONTOSAURUS LESINENSIS AND THE EVALUATION OF ...

ISBN 0-612-82329-6
MQ-82329

caudal vertebrae (69, 0.5, 0→1), caudal neural spines taller than dorsal neural spines, tail dorsoventrally expanded (70, 0.5, 0→1).

Dolichosauridae: Dolichosaurus, Coniasaurus crassidens, Coniasaurus gracilodens.

Maxilla, premaxillary process large and extending medially from anterior end of maxilla (7, 1.0, 0→1), maxilla-premaxilla contact anterior end free (8, 0.75, 0→1), medial descending process of frontal present (14, 0.5, 0→1), frontal shape long and broad anteriorly, constricted orbital margin (16, 0.667, 0→2), supraoccipital posterior to parietal, forms part of skull roof (40, 0.667, 0→1), marginal teeth without sharp carinae (54, 0.5, 0⇒1), tooth crown inflation present (58, 1.0, 0⇒1), neural spines on dorsal vertebrae reduced to low ridges (60, 0.5, 0→1), number of presacral vertebrae between 34 and 50 (63, 1.0, 0→1), number of cervical vertebrae nineteen or more (64, 0.667, 0→2), condyles circular and cotyles oval (65, 0.5, 0→2), one pygal (68, 0.6, 0→2), anterior coracoid emargination absent (73, 1.0, 0⇒1).

Clade B: Aphanizocnemus, Acteosaurus, Eidolosaurus, Pontosaurus, MSNM V3662, Adriosaurus, and Ophidia.

Frontal shape long and broad anteriorly, constricted orbital margin (16, 0.667, 0→2), quadrate 'circular' in lateral view (36, 0.5, 0→1), marginal teeth without sharp carinae (54, 0.5, 0→1), neural spines on dorsal vertebrae reduced to low ridges (60, 0.5, 0→1), number of presacral vertebrae between 34 and 50 (63, 1.0, 0→1), one pygal vertebrae (68, 0.6, 0→2), forelimb larger than hind limb (76, 1.0, 0→1).

Clade C: Acteosaurus, Eidolosaurus, Pontosaurus, MSNM V3662, Adriosaurus, and Ophidia.

Number of cervical vertebrae between 10 and 12 (64, 0.667, 0→1), proximal portion of olecranon absent (75, 0.333, 0→1), manus/pes as long as propodials/ epipodials (77, 0.5, 0→1).

Clade D: Eidolosaurus, Pontosaurus, MSNM V3662, Adriosaurus, and Ophidia.

Maxilla, premaxillary process large and extending medially from anterior end of maxilla (7, 1.0, 0→1), maxilla-premaxilla contact free anteriorly (8, 0.75, 0→1), parietal dorsal surface as long as frontal (19, 0.667, 0→1), descensus parietalis prominent flanges not contacting basisphenoid (20, 1.0, 0→1), quadrate tympanic crest directed laterally and a well-developed wall (37, 1.0, 0→1), supraoccipital situated posterior to parietal, forms part of posterior skull roof (40, 0.667, 0→1), retroarticular process with medial flange (53, 0.5, 0→1), scapula-coracoid fused (72, 1.0, 0→1), forelimb smaller than hind limb (76, 1.0, 1→2), pubis not expanded distally (79, 1.0, 0→1), fibula distal end expanded (80, 0.5, 0→1).

Clade E: Eidolosaurus and Pontosaurus.

Pachyostosis present in mid-dorsal vertebrae (67, 0.5, 0→1), epipodials distally diverging (74, 1.0, 0→1).

Clade F: MSNM V3662, Adriosaurus, and Ophidia.

Anterior end of premaxilla with lateral flange (2, .5, 0→1), dorsal process of maxilla on middle or anterior end of maxilla (9, 1.0, 0→1), lacrimal absent (11, 1.0, 0→1), frontal without sagittal crest (17, 0.5, 1→0), parietal table a narrow sagittal crest, jaw adductors extend over entire dorsal surface of parietal (21, 1.0, 0→1), suspensorial ramus extremely short or absent (23, 1.0, 0⇒1), supratemporal large and extending onto parietal table (27, 1.0, 0⇒1), postorbital ventral process prominent, forming half or more of posterior orbital margin (30, 0.5, 0→1), anterior end of vomer entirely medial to palatine (41, 0.333, 0→1), posterior border of opening for jacobson's organ closed by contact with vomer and septomaxilla (42, 1.0, 1→2), palatine-vomer with mobile contact (43, 1.0, 0→1), palatine–maxilla loose joint or no contact (44, 1.0, 0→1), intramandibular septum of meckel's canal poorly developed (46, 1.0, 0→1), mental foramina on lateral surface of dentary two or fewer (47, 1.0, 0→1), splenial-angular contact not or very slightly exposed in lateral view (48, 0.5, 1→0), splenial widely separate from anteromedial margin of coronoid (49, 0.5, 1→2), surangular with long anterior projection that projects into a deep notch in the dentary (51, 1.0, 0→1), articular fused with prearticular and surangular (52, 1.0, 0→2), marginal teeth without sharp carinae (54, 0.5, 1→0), palatine toothed (55, 0.5, 0→1), zygapophyses of mid-trunk vertebrae moderately inclined medially (59, 1.0, 0→1), ribs begin from third or more anterior cervical vertebrae (61, 0.5, 0⇒1), condyles and cotyles circular (65, 0.5, 0→1), condyles of dorsal vertebrae vertical (66, 0.5, 0→1), pachyostosis of mid-dorsal vertebrae

present (67, 0.5, 0→1), pygals four or more (68, 0.6, 2→0), epipodials distally diverging (74, 1.0, 0→1).

Clade G: Adriosaurus and Ophidia (Pachyrhachis, Haasiophis, Dinilysia, Scolecophidia, and Alethinophidians).

Maxilla-premaxilla connected by a short ligament or widely separate (8, 0.75, 1→2), frontoparietal suture complex curved or interdigitating (18, 1.0, 0⇒1), quadrate articulates dorsally with supratemporal, little or no contribution from other elements (35, 1.0, 0→1), quadrate without elaborated suprastapedial and infrastapedial process (36, 0.5, 1→0), quadrate tympanic crest absent and external surface only weakly concave (37, 1.0, 1→2), two pygals (68, 0.6, 0→1).

Ophidia: Pachyrhachis, Haasiophis, Dinilysia, Scolecophidia, and Alethinophidians.

Maxilla, premaxillary process absent (7, 1.0, 1⇒2), posterior process of maxilla long, extending past middle or ventral margin of orbit (10, 1.0, 0⇒1), frontals paired (13, 0.5, 1⇒0), frontal broad and rectangular, straight orbital margin (16, 0.667, 2⇒1), descensus parietalis prominent flanges contacting basisphenoid (20, 1.0, 1⇒2), parietal foramen absent (24, 1.0, 0⇒1), upper temporal arch incomplete (25, 1.0, 0⇒1), anteroventral border of orbit formed by maxilla (31, 1.0, 0⇒1), squamosal absent (32, 1.0, 0⇒1), epipterygoid absent (45, 1.0, 0⇒1), surangular fused with articular, contribution to articular cotyle cannot be determined (50, 0.667, 0→2), retroarticular process simple, without medial flange (53, 0.5, 1→0), number of presacral vertebrae 120

or more (63, 1.0, 1⇒2), number of cervical vertebrae nineteen or more (64, 0.667, 1⇒2), caudal transverse processes present on all caudal vertebrae (69, 0.5, 1→0), caudal neural spines no taller than dorsal neural spines, tail not dorsoventrally expanded (70, 0.5, 1⇒0), fibula distal end not expanded (80, 0.5, 1→0).

Clade H: Haasiophis, Dinilysia, Scolecophidia, and Alethinophidians.

Anterior end of maxilla without lateral flange (2, 0.5, 1→0). parietal dorsal surface longer than frontal (19, 0.667, 1⇒2), postfrontal not forked medially (29, 1.0, 0⇒1), jugal absent (33, 1.0, 0⇒1), lymphapophyses present (62, 1.0, 0⇒1), pelvis internal to sacral or cloacal ribs (78, 1.0, 0⇒1).

Clade I: Dinilysia, Scolecophidia, and Alethinophidians.

Postorbital and postfrontal separate ossifications (28, 0.75, 0→1), exoccipitals extensive median contact above foramen magnum (39, 1.0, 0⇒1), vomer anterior or anteromedial to palatine (41, 0.333, 1→0), pachyostosis of mid-dorsal vertebrae absent (67, 0.5, 1⇒0).

Serpentes: Scolecophidia and Alethinophidia.

External naris slightly retracted, prefrontal, but not frontal, enters posterior narial margin (4, 1.0, 0⇒1), nasal and prefrontal bones contact (5, 1.0, 0⇒1), maxilla-premaxilla suture or strongly abutting (8, 0.75, 2→0), descensus frontalis abutting each other or contacting parabasisphenoid below olfactory tract (15, 1.0, 0⇒1).

Discussion—The phylogenetic analysis presented here indicates that dolichosaurs are more closely related to snakes than to other marine lizards. A dolichosaur-snake relationship is fairly well supported in the current study with 64 percent of 1000 bootstrap replicates recovering this association (Clade A). This phylogenetic conclusion is in accord with recent findings by Lee and Caldwell (2000) and Pierce and Caldwell (2002) and further substantiates Nopcsa's (1908; 1923) claim of a close evolutionary relationship between dolichosaurs and snakes. Consequently, it appears as though snakes are nested deeply within a radiation of elongate, limb reduced, marine squamates. The results of this analysis, therefore, continue to provide support for the marine origins hypothesis of snake origins and seem to suggest that marine habits are primitive for snakes.

Results from the analysis further reveal the same overall pattern of relationships as reported by Lee and Caldwell (2000) and Pierce and Caldwell (2002). Dolichosaurs appear as a non-monophyletic group that form successive sister taxa to snakes (Fig. 2-1). However, this outcome is poorly supported. The series of more exclusive dolichosaur-snake clades (Clades B-D, F and G) are recovered in only 30-37 percent of 1000 bootstrap replicates. These low bootstrap values are probably a function of the large amount of equivocal characters supporting the clades. In fact, many of the new characters and character states identified for dolichosaurs in this analysis diagnose several clades. For example, characters 7 (state 1) and 8 (state 1) are recovered as synapomorphies for both the Dolichosauridae and Clade D. Moreover, many of the characters diagnosing Clade E and Clade F are snake synapomorphies, which cannot be observed in either MSNM V3662 or Adriosaurus due to poor preservation. Therefore,

the hypothesis that dolichosaurs are a non-monophyletic group that form successive sister taxa to snakes is still highly tentative.

In terms of the specific pattern of dolichosaur interrelationships, the current analysis somewhat modifies the conclusion reached by Lee and Caldwell (2000) and Pierce and Caldwell (2002). In these two previous studies an unresolved dichotomy remained between the Dolichosauridae (a terminal taxon combining the osteological features of Dolichosaurus and Coniasaurus) and Aphanizocnemus. In contrast, the present study finds resolution between these two taxa (Clade B). Additionally, based on the results of Pierce and Caldwell (2002), Pontosaurus was the sister taxon to the Adriosaurus-snake clade. This is not the case in the present study, which finds an undescribed specimen of a dolichosaur, MSNM V3662, as the sister taxon. Consequently, Pontosaurus moves down one node and forms a clade with Eidolosaurus (Clade E). However, only two equivocal characters support Clade E (the presence of pachyostosis and distally diverging epipodials) both of which are also found in Adriosaurus and MSNM V3662.

Although the incorporation of the eight identified dolichosaur species into one family is inaccurate, the dissolution of the Dolichosauridae is not warranted. Kramberger (1892) originally created the family for the monotypic species Dolichosaurus longicollis. Nopcsa (1903) subsequently added Acteosaurus tommasinii, Pontosaurus lesinensis, and Adriosaurus suessi to the family based on anatomical similarities between these Adriatic lizards and Dolichosaurus. The analysis presented here finds that Dolichosaurus does not form a monophyletic group with these Adriatic species, though it does form a relatively well-supported clade (bootstrap value of 54) with Coniasaurus. Consequently, the family

Dolichosauridae is here revised to include only Dolichosaurus longicollis, Coniasaurus crassidens, and Coniasaurus gracilodens (Fig. 2-1). However, as noted by Caldwell (2000), our current knowledge of the anatomy in Dolichosaurus and Coniasaurus is problematic as Dolichosaurus is recognized primarily by postcranial material and Coniasaurus by cranial material. Hence, there exists a possibility that these taxa are congeneric and the family Dolichosauridae consists of only one genus and two species. If this is the case, the polytomy (Fig. 2-1) currently obscuring reconstructions of Dolichosaurus-Coniasaurus relationships would disappear.

This study was designed to examine dolichosaur affinities; however, it also inadvertently assessed the interrelationships of snakes. The primary analysis ascertained that fossil snakes form successive sister taxa to the Serpentes (Pachyrhachis (Haasiophis (Dinilysia))), with Pachyrhachis as the most basal snake (Fig. 2-1). This is intriguing considering the controversy over the phylogenetic position of fossil snakes. Depending on how the osteological features of fossil snakes are interpreted and what data matrix they are added to, fossil snakes are reconstructed as either the sister taxa to modern snakes (Caldwell and Lee, 1997; Lee and Caldwell, 1998; 2000; Lee, 1998; Caldwell, 1999a; Lee et al., 1999; Cohn and Tickle, 1999; Rage and Escuillié, 2000; Lee and Scanlon, 2002) or as derived snakes nested within Serpentes (Zaher, 1998; Zaher and Rieppel, 1999; 2000; Rieppel and Zaher, 2000; Tchernov et al., 2000). The current study analyzed a data matrix that was modified with respect to dolichosaur anatomy; in other words, no attention was placed on discerning characters that would help to resolve snake relationships. Consequently, the results of the primary analysis (Test 1) provide additional support for the basal position of fossil snakes.

Test 2: All fossil and modern snakes excluded (5 taxa)

Results—A Branch-and-Bound search of 12 taxa and 80 characters resulted in 3 shortest cladograms (86 steps) with a Consistency Index (C.I.) of 0.85, a refined C.I excluding 21 uninformative characters of 0.79, and a Retention Index (R.I.) of 0.79. The same tree topology (minus the snakes) as Test 1 was recovered in both the strict consensus tree and the 50% majority-rule consensus tree (Fig. 2-2).

Discussion—The origin and evolution of snakes remains unresolved. Current hypotheses concerning snake interrelationships fall within two broad categories (Coates and Ruta, 2000; Rieppel and Kearney, 2001). One view is that snakes are descended from terrestrial squamates that developed fossorial habits (Zaher, 1998; Zaher and Rieppel, 1999; 2000; Rieppel and Zaher, 2000). The alternative proposes a close evolutionary relationship between snakes and marine lizards (Caldwell and Lee, 1997; Lee and Caldwell, 1998; 2000; Lee, 1997; 1998; Caldwell, 1999a; Cohn and Tickle, 1999; Lee et al., 1999; Lee and Scanlon, 2002). By adding snakes to the current analysis, the pythonomorph affinities and 'marine' scenario of snake origins are presumed. Therefore, snakes were isolated out of the analysis to ascertain if they were having a negative affect on dolichosaur interrelationships. The removal of all snakes from the analysis, however, did not change the overall pattern of relationships (Fig. 2-2). Therefore, Test 1 appears to be fairly robust and stable with respect to dolichosaur phylogeny. This is a significant finding in light of the two opposing views concerning snake affinities. Test 2 suggests that even if snakes are not part of the ingroup in this

study, their inclusion into the analysis does not disrupt or alter the phylogenetic distribution of dolichosaurs.

Test 3: All fossil snakes excluded (3 Taxa)

Results—A Branch-and-Bound search of 14 taxa and 80 characters resulted in 6 shortest cladograms (139 steps) with a Consistency Index (C.I.) of 0.77, a refined C.I excluding 7 uninformative characters of 0.76, and a Retention Index (R.I.) of 0.74. Both the strict consensus tree and the 50% majority-rule consensus tree (Fig. 2-3) recover a major polytomy in the ingroup. The only resolved clades are the Mosasauroidea, the Dolichosauridae, Clade E (Eidolosaurus and Pontosaurus), and Serpentes.

Discussion—The anatomical characteristics of fossil snakes are a matter of debate. Certain features preserved on the fossils have been interpreted and coded in data matrices in dramatically different ways. This discrepancy causes noticeable differences in cladogram structure; fossil snakes can either end up basal with respect to modern snakes or derived and nested within the modern snake clade (see above). Thus, fossil snakes were removed from the analysis to discover whether the pattern of relationships between dolichosaurs and snakes are influenced by their presence in the data matrix. By excluding fossil snakes from the analysis the relationship between mosasauroids, dolichosaurs, and snakes becomes uncertain (Fig. 2-3). It has been argued that certain taxa, fossil and/or extant, act as 'keystone' taxa that significantly affect tree topology (Caldwell, 1999a). The results of Test 3 imply that fossil snakes are key to resolving pythonomorph interrelationships. But, which fossil snake(s) is the pivotal taxon?

Test 3A: Sequential addition of fossil snakes

1) Addition of Pachyrhachis: The same tree topology as Test 3 is recovered, except Pachyrhachis is found as the sister taxon to Serpentes (Fig. 2-4A).

2) Addition of Haasiophis: Dolichosaurs become a monophyletic group and position as the sister group to mosasauroids. The pattern of relationships among dolichosaurs is consistent with Test 1. The mosasauroid-dolichosaur clade is the sister group to snakes with scolecophidians as the most basal snakes (Fig. 2-4B).

3) Addition of Dinilysia: Dolichosaurs become a monophyletic group and position as the sister group to mosasauroids. The pattern of relationships among dolichosaurs is consistent with Test 1. The mosasauroid-dolichosaur clade is the sister group to snakes with scolecophidians as the most basal snakes (Fig. 2-4C).

4) Addition of Pachyrhachis and Haasiophis: The same tree topology as Test 1 is recovered (Fig. 2-4D).

5) Addition of Pachyrhachis and Dinilysia: The same tree topology as Test 1 is recovered (Fig. 2-4E).

6) Addition of Haasiophis and Dinilysia: Dolichosaurs become a monophyletic group and position as the sister group to mosasauroids. The pattern of relationships among dolichosaurs is consistent with Test 1. The mosasauroid-dolichosaur clade is the sister group to snakes. Scolecophidians are recovered as the most basal snake and Dinilysia is found to be the sister taxon to a clade containing alethinophidians and Haasiophis (Fig. 2-4F).

From these additional tests it appears as though Pachyrhachis is not a keystone taxon on its own (Fig. 2-4A); however, when Pachyrhachis is accompanied by another

fossil snake the same tree topology as Test 1 is recovered (Fig. 2-4D,E). In contrast, the addition of either Haasiophis and/or Dinilysia resolves the cladogram, but the interrelationships of the Pythonomorpha are substantially different from Test 1 (Fig. 2-4B, C, F); dolichosaurs become a monophyletic group more closely related to mosasauroids than to snakes and fossil snakes appear derived with respect to modern snakes. Consequently, Test 3 and 3A suggest that a close evolutionary relationship between dolichosaurs and snakes to the exclusion of mosasauroids is fairly unstable and completely reliant on which fossil snakes are included in the analysis. On the other hand, Test 3A further supports Test 1 with respect to the overall pattern of relationships among the dolichosaur taxa.

Test 4: Mosasauroids excluded (2 Taxa)

Results—A Branch-and-Bound search of 15 taxa and 80 characters resulted in 24 shortest cladograms (125 steps) with a Consistency Index (C.I.) of 0.76, a refined C.I excluding 8 uninformative characters of 0.74, and a Retention Index (R.I.) of 0.78. The strict consensus tree and 50% majority-rule consensus tree (Fig. 2-5) recover two clades, one consisting of all dolichosaurs and the other of all snakes. The pattern of relationships observed among the dolichosaur taxa is similar to Test 1, except Eidolosaurus, Pontosaurus, MSNM V3662, collapse into a polytomy. The pattern of relationships observed among snakes, however, is significantly different than Test 1; scolecophidians are the most basal snake and all fossil snakes form a polytomy with alethinophidians.

Discussion—A close evolutionary relationship between mosasauroids and dolichosaurs has long been presumed. As a result, dolichosaurs have always been incorporated into a data matrix that included mosasauroids (Dal Sasso and Pinna, 1997; Caldwell, 1999a,b; Caldwell, 2000; Lee and Caldwell, 2000; Pierce and Caldwell, 2002). By excluding mosasauroids from the analysis, Test 4 investigates how these marine lizards influence the interrelationships of dolichosaurs and snakes. The results show two dramatic changes from the cladogram recovered in Test 1 (Fig. 2-5). First, dolichosaurs become a monophyletic clade with respect to snakes (similar to Test 3A). In this sense, mosasauroids appear to function as a character anchor by distributing the mosaic of mosasauroid-like and snake-like characteristics observed in dolichosaurs along the cladogram. Second, scolecophidians become the most basal snake with all fossil snakes nested within Serpentes (similar to Test 3A). This pattern of snake interrelationships is expected because the suite of synapomorphies that were previously uniting dolichosaurs and snakes no longer exists. Consequently, fossil snakes appear to be more similar to alethinophidian snakes, which in turn, forces the highly specialized scolechophidian snakes into a basal position. Although the topology of the tree in Test 4 is different with respect to dolichosaur-snake relationships, the overall pattern of relationships among dolichosaurs remains similar to Test 1.

Test 5: Pachyostosis (character 67) excluded

Results—A Branch-and-Bound search of 17 taxa and 79 characters resulted in 6 shortest cladograms (150 steps) with a Consistency Index (C.I.) of 0.72 and a Retention

Index (R.I.) of 0.80. The same tree topology as Test 1 was recovered in both the strict consensus tree and the 50% majority-rule consensus tree (Fig. 2-1).

Discussion—Pachyostosis or a thickening of the periosteal bone is an anatomical adaptation restricted to secondarily aquatic vertebrates (reptiles and mammals). It functions to create neutral buoyancy in shallow diving animals by counteracting the buoyancy created by the air filled lungs (Scanlon et al., 1999; Lee and Caldwell, 2000). This feature of the skeleton is manifested in some dolichosaurs (Eidolosaurus, Pontosaurus, MSNM V3662, and Adriosaurus) and fossils snakes (Pachyrhachis and Haasiophis). As a result, the pachyostosis character was removed from the analysis to determine if the relationship between dolichosaurs and snakes was being influence by a skeletal feature that can appear randomly in a variety of secondarily aquatic animals. Removal of the pachyostosis character from the analysis, however, had no effect on the cladogram recovered in Test 1 (Fig. 2-1). Therefore, it appears that the pattern of relationships observed among dolichosaurs and between dolichosaurs and snakes in Test 1 is dependent on a variety of osteological features other than pachyostosis.

CONCLUSIONS

The results of the primary analysis indicate: 1) dolichosaurs are more closely related to snakes than to other marine lizards, 2) dolichosaurs are a non-monophyletic group that form successive sister taxa to snakes, and 3) fossil snakes are primitive. These conclusions, however, remain tentative. By manipulating certain taxa in the analysis dolichosaurs become a monophyletic group more closely related to mosasauroids than to

snakes. Additionally, fossil snakes alternate between being primitive and derived with respect to modern snakes. Conversely, the same overall pattern of relationships among the different dolichosaur taxa is constant in all analyses. This outcome suggests that dolichosaur interrelationships are quite robust and stable and independent of whether the group is monophyletic, non-monophyletic, the sister group of snakes, or the sister group of mosasauroids.

Because the current study is the first in the discipline to examine dolichosaur interrelationships in depth, the phylogenetic conclusions presented here are preliminary. Although this study greatly enhances our understanding of dolichosaur anatomy and phylogeny, a large amount of missing information still exists. For instance, right now the majority of dolichosaur species are only known from a single specimen; this creates a small sample size and leaves many aspects of dolichosaur anatomy undiscovered. Consequently, to elucidate the evolutionary affinities of dolichosaurs more accurately new material needs to be actively collected and thoroughly analyzed.

FIGURE 2-1. Test 1. The strict consensus/50% majority-rule consensus tree of 3 trees recovered from a Branch-and-Bound search of all 17 taxa and 80 characters. Tree length = 152; C.I. = 0.72; R.I. = 0.80. Bootstrap values appear in brackets. An identical tree was recovered for Test 5, the exclusion of Character 67 or pachyostosis. See text for discussion.

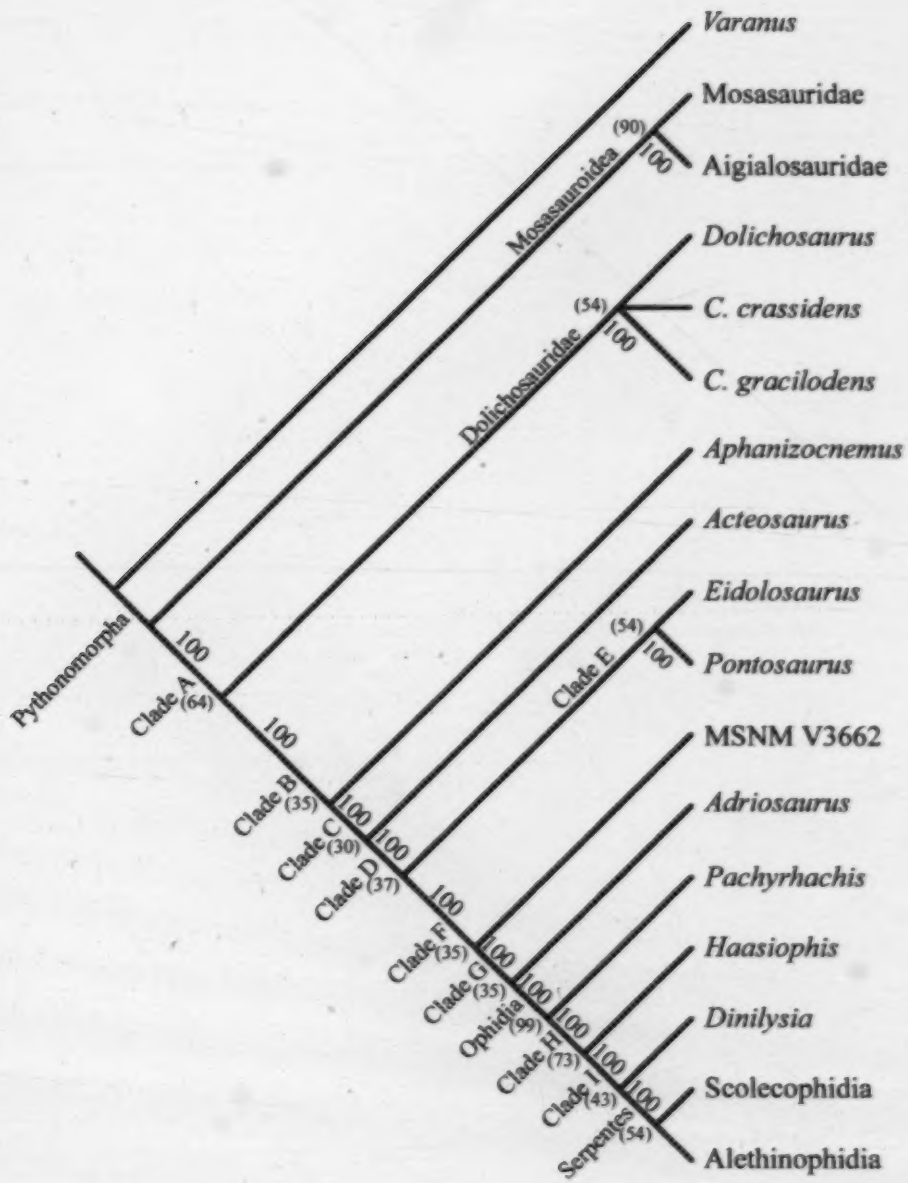

Varanus
Mosasauridae
(90)
100
Aigialosauridae
Mosasauroidea
Dolichosaurus
(54)
C. crassidens
100
C. gracilodens
Dolichosauridae
Aphanizocnemus
Acteosaurus
Eidolosaurus
(54)
Pontosaurus
100
Clade E
MSNM V3662
Adriosaurus
Pachyrhachis
Haasiophis
Dinilysia
Scolecophidia
Alethinophidia
Pythonomorpha
100
Clade A
(64)
100
Clade B
(35)
100
Clade C
(30)
100
Clade D
(37)
100
Clade F
(35)
100
Clade G
(35)
100
Ophidia
(99)
100
Clade H
(73)
100
Clade I
(43)
100
Serpentes
(54)

FIGURE 2-2. Test 2. The strict consensus/50% majority-rule consensus tree of 3 trees from a Branch-and-Bound search with all fossil and modern snakes excluded. Tree length = 86 steps; C.I. = 0.85; C.I excluding 21 uninformative characters = 0.79, R.I. = 0.79. See text for discussion.

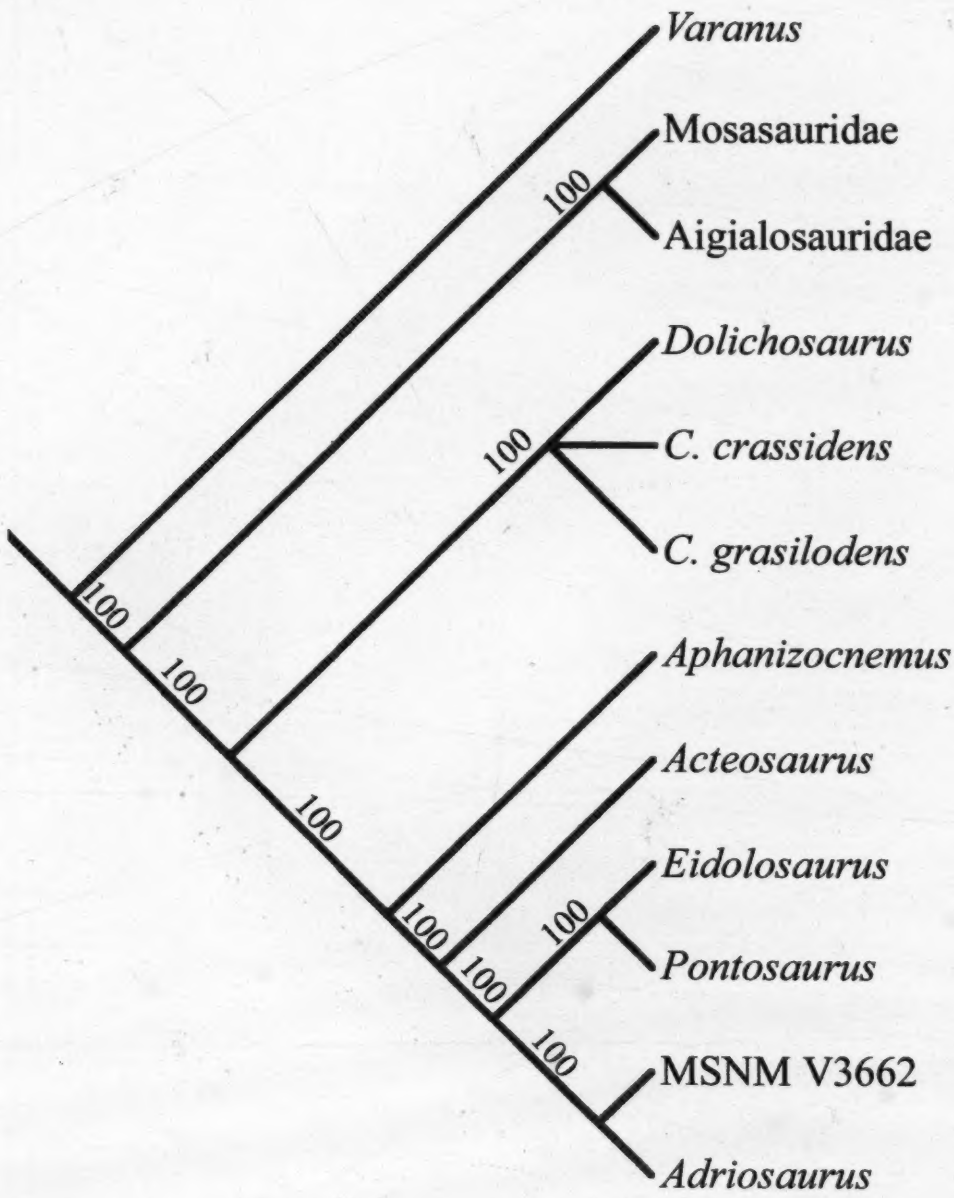

Varanus
Mosasauridae
Aigialosauridae
Dolichosaurus
C. crassidens
C. grasilodens
Aphanizocnemus
Acteosaurus
Eidolosaurus
Pontosaurus
MSNM V3662
Adriosaurus
100
100
100
100
100
100
100
100
100

FIGURE 2-3. Test 3. The strict consensus/50% majority-rule consensus tree of 6 trees from a Branch-and-Bound search with all fossil snakes excluded. Tree length = 139; C.I. = 0.77, C.I excluding 7 uninformative characters = 0.76, R.I. = 0.74. See text for discussion.

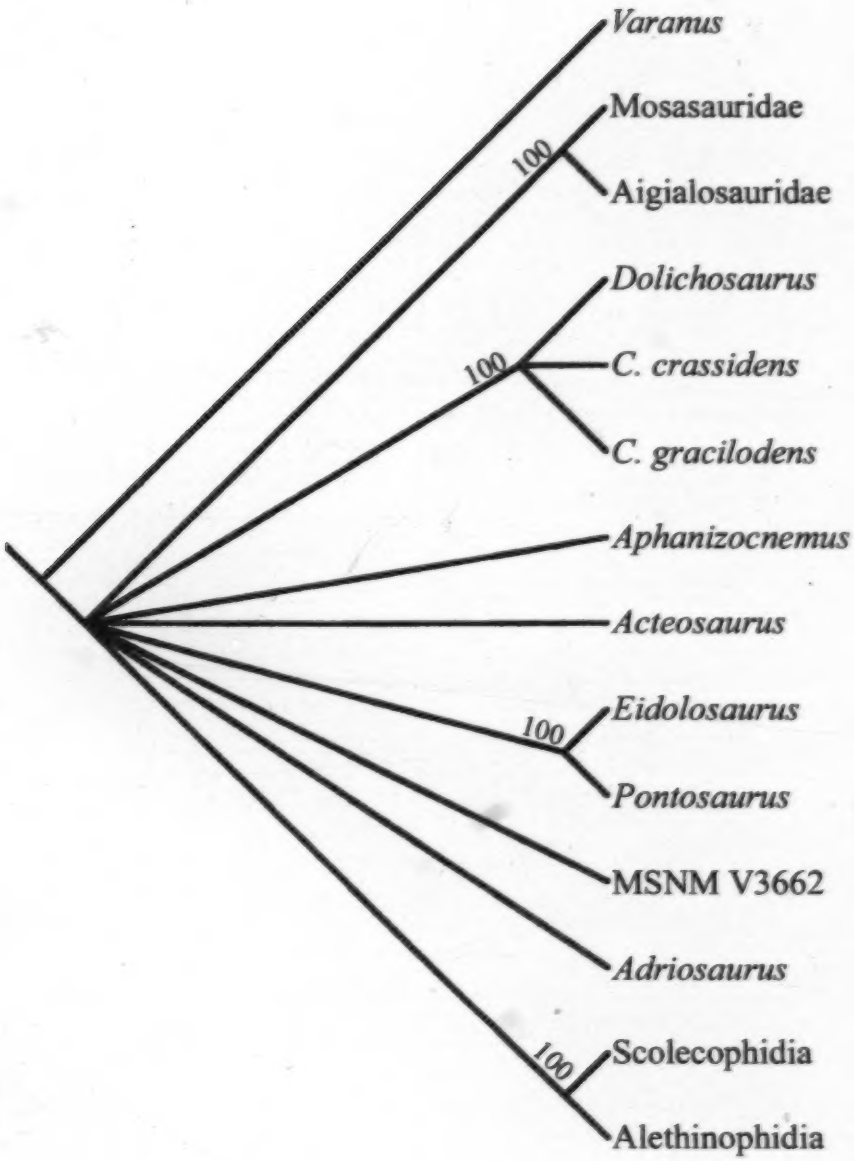
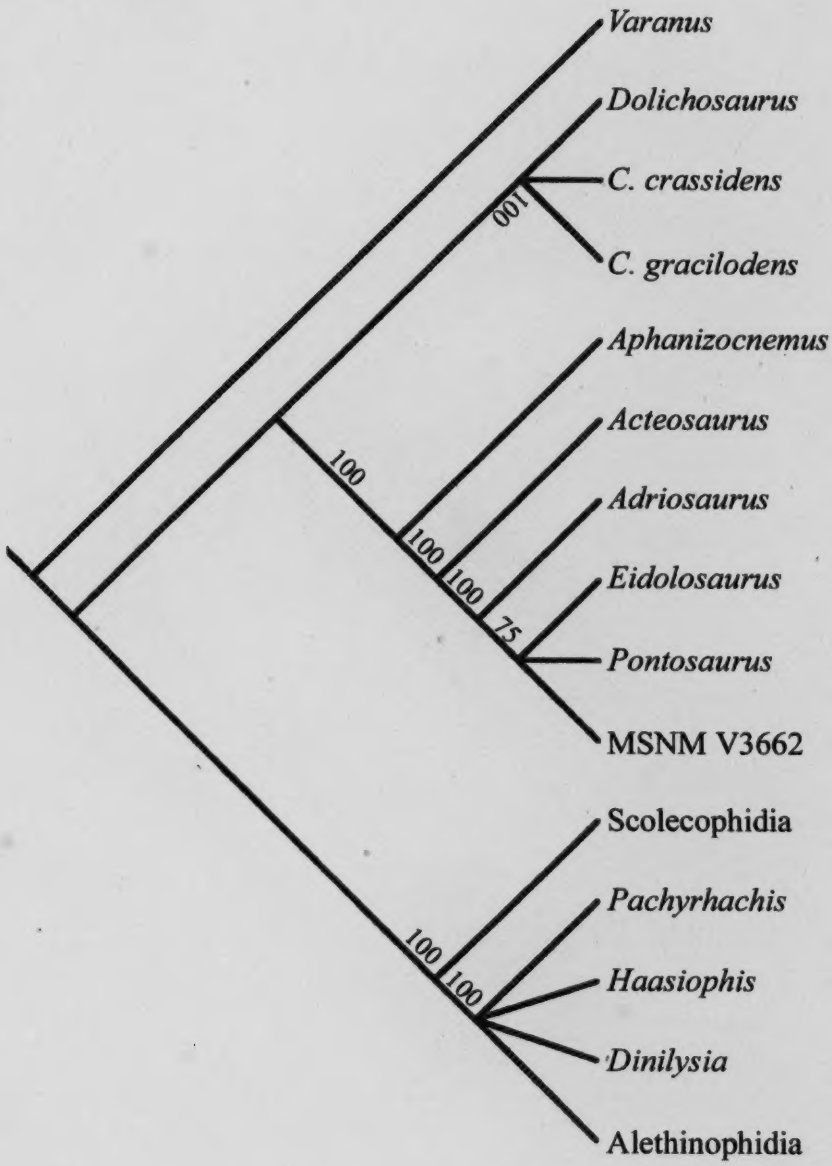

Varanus
Mosasauridae
100
Aigialosauridae
Dolichosaurus
100
C. crassidens
C. gracilodens
Aphanizocnemus
Acteosaurus
Eidolosaurus
100
Pontosaurus
MSNM V3662
Adriosaurus
Scolecophidia
100
Alethinophidia

FIGURE 2-4. Test 3A. The strict consensus/50% majority-rule consensus trees from the sequential addition of fossil snakes back into the analysis. **A,** Addition of Pachyrhachis; **B,** Addition of Haasiophis; **C,** Addition of Dinilysia; **D,** Addition of Pachyrhachis and Haasiophis; **E,** Addition of Pachyrhachis and Dinilysia; **F,** Addition of Haasiophis and Dinilysia. See text for discussion.

Varanus
Mosasauridae
Aigialosauridae
Dolichosaurus
C. crassidens
C. gracilodens
Aphanizocnemus
Acteosaurus
Eidolosaurus
Pontosaurus
MSNM V3662
Adriosaurus
Pachyrhachis
Scolecophidia
Alethinophidia
A
Varanus
Mosasauridae
Aigialosauridae
Dolichosaurus
C. crassidens
C. gracilodens
Aphanizocnemus
Acteosaurus
Eidolosaurus
Pontosaurus
MSNM V3662
Adriosaurus
Scolecophidia
Haasiophis
Alethinophidia
B
Varanus
Mosasauridae
Aigialosauridae
Dolichosaurus
C. crassidens
C. gracilodens
Aphanizocnemus
Acteosaurus
Eidolosaurus
Pontosaurus
MSNM V3662
Adriosaurus
Scolecophidia
Dinilysia
Alethinophidia
C

Varanus
Mosasauridae
Aigialosauridae
Dolichosaurus
C. crassidens
C. gracilodens
Aphanizocnemus
Acteosaurus
Eidolosaurus
Pontosaurus
MSNM V3662
Adriosaurus
Pachyrhachis
Haasiophis
Scolecophidia
Alethinophidia
D
Varanus
Mosasauridae
Aigialosauridae
Dolichosaurus
C. crassidens
C. gracilodens
Aphanizocnemus
Acteosaurus
Eidolosaurus
Pontosaurus
MSNM V3662
Adriosaurus
Pachyrhachis
Dinilysia
Scolecophidia
Alethinophidia
E
Varanus
Mosasauridae
Aigialosauridae
Dolichosaurus
C. crassidens
C. gracilodens
Aphanizocnemus
Acteosaurus
Eidolosaurus
Pontosaurus
MSNM V3662
Adriosaurus
Scolecophidia
Dinilysia
Haasiophis
Alethinophidia
F

FIGURE 2-5. Test 4. The strict concsensus/50% majority-rule consensus tree of 24 trees from a Branch-and-Bound search with mosasaurs and aigialosaurs excluded. Tree length = 125 steps; C.I. = 0.76, C.I excluding 8 uninformative characters = 0.74, R.I. = 0.78. See text for discussion.


Varanus
Dolichosaurus
C. crassidens
C. gracilodens
Aphanizocnemus
Acteosaurus
Adriosaurus
Eidolosaurus
Pontosaurus
MSNM V3662
Scolecophidia
Pachyrhachis
Haasiophis
Dinilysia
Alethinophidia
100
100
100
100
100
75
100
100

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APPENDIX I

Character List

Characters and character states identified for the ingroup; only characters that could be coded for at least one dolichosaur terminal taxon were utilized. Letters and numbers in parentheses indicate the articles where the characters have previously been used in cladistic analyses that examined some aspect of pythonomorph interrelationships: **(DC3/DP7)**, DeBraga and Carroll, 1993/Dal Sasso and Pinna, 1997; **(CCK5)**, Caldwell, Carroll and Kaiser, 1995; **(C6)**, Caldwell, 1996; **(L7)**, Lee, 1997; **(C9)**, Caldwell, 1999a; **(C-9)**, Caldwell, 1999b; **(C0)**, Caldwell, 2000; **(LC0)**, Lee and Caldwell, 2000; **(L-2)**, Lee, 2002. Most characters are discussed in these papers or reference the original paper where the character was developed and are only briefly listed here. New or modified characters informative for the different set of terminal taxa are identified by an asterisk (*). Where necessary the codings for dolichosaurs are discussed under the relevant character.

(a) skull roof

1. **Premaxilla-** Does not contact frontals (0); contacts frontals (1). **(LC0; L7)** There is a definite contact between the internarial bar of the premaxilla and the frontal in MSNM V3662. The contact in Pontosaurus is not preserved, however, there is a significant gap between the nasal bones implying that the internarial bar of the premaxilla has been broken at its posterior extent and must have contacted the frontal.
2. **Anterior end of premaxilla-** Without lateral flange (0); with lateral flange (1).

In Pontosaurus, Adriosaurus, and MSNM V3662, the anterior end of the premaxilla is not rounded as in mosasauroids and Varanus, but rather laterally expanded into an oval shaped disk, a similar configuration to some alethinophidian snakes. This lateral flange is also present in Pachyrhachis and Dinilysia. The premaxilla in Haasiophis is small and narrow and does not appear to have a lateral flange.

3. **Nasals**- Large (0); reduced or absent (1). **(DC3/DP7; L7; LC0)**

   Compared to mosasaurs, Pontosaurus and MSNM V3662 have rather large nasals that run almost the entire length of the premaxillary internarial bar to contact the frontal posteriorly. The frontal in Coniasaurus has a large articulatory surface for the nasal bones suggesting that the nasals were also fairly large.

4. **External naris**- Greatly retracted, prefrontal and frontal enter posterior narial margin (0); Slightly retracted, prefrontal (but not frontal) enters posterior narial margin (1). **(L7; LC0)**

   The prefrontal and frontal does enter the external narial opening in Haasiophis and Dinilysia.

5. **Nasal and prefrontal bones contact**- Absent (0); present (1). **(CCK5; C-9; LC0)**

6. **Septomaxilla-maxilla contact**- Rigid, septomaxilla extensively sutured to the dorsal surface of the palatal flange of the maxilla (0); mobile, septomaxilla not sutured to maxilla (1). **(LC0)**

7. ***Maxilla, premaxillary process**- Present, horizontal flange on medial surface of anterior end of maxilla (0); present, large premaxillary process extending

medially from anterior end of maxilla (1); absent, anterior end of maxilla without such flange/process (2). **(L7; LCO; L-2)**

The premaxillary process in Coniasaurus and MSNM V3662 is shaped like a small, rounded, blunt tooth. It extends medially and anteriorly from the maxillary wall, just above the dental shelf. The appearance of the process suggests it could have functioned as a pivot point for a potentially mobile maxillary-premaxillary contact (see next character) (Caldwell, 1999a).

8. ***Maxilla-premaxilla contact**- Suture or strongly abutting (0); anterior end free (1); connected by a short ligament or widely separated (2). **(L-2)**

The anterior end of the premaxilla appears to be free of a contact with the maxilla in Pontosaurus, Adriosaurus, and MSNM V3662; based on the excellent preservation in MSNM V3662, the premaxilla loosely contacts the premaxillary process of the maxilla behind the anterior lateral flange. Although the premaxilla is not preserved in Coniasaurus, the presence of a large premaxillary process implies that the maxilla-premaxilla contact was similar.

9. **Dorsal process of maxilla**- On posterior half of maxilla (0); on middle or anterior end of maxilla (1). **(L7; LC0)**

The dorsal process of the maxilla in Coniasaurus is unmistakably on the posterior end of the maxilla; however, the dorsal process of the maxilla in Pontosaurus appears to be on the middle of the maxilla, a condition only observed in snakes. The preservation of the maxilla in Adriosaurus is to poor to code contra Lee and Caldwell (2000) who suggested the dorsal process to be on the posterior half of the maxilla.

10. **Posterior process of maxilla**- Short, not reaching middle of ventral margin of orbit (0); long, reaching or extending past middle of ventral margin of orbit (1). **(L7; LC0)**

11. **Lacrimal**- Present (0); absent (1). **(L7; LC0)**

    There is no evidence of a lacrimal in Pontosaurus and MSNM V3662; the jugal in both genera contacts the prefrontal directly. Although Lee and Caldwell (2000) coded Adriosaurus with a lacrimal, there is no evidence of a lacrimal on either side of the skull. Coniasaurus, however, appears to have a facet for the articulation of a lacrimal.

12. **Prefrontal**- Without antorbital ridge (0); with antorbital ridge extending from anterodorsal margin of orbit towards external naris (1). **(DC3/DP7; L7; LC0)**

13. **Frontals**- Unfused, paired element (0); fused into single median element (1). **(DC3/DP7; CCK5; L7; C-9; LC0)**

    Pontosaurus, Aphanizocnemus, Coniasaurus, and MSNM V3662 all have a fused frontal. The frontal in Adriosaurus has been described as a paired element, however, this is more likely a taphonomic artefact. Adriosaurus is coded as having a fused frontal contra Lee and Caldwell (2000).

14. **Medial descending process of frontal**- Absent (0); present (1). **(L-2)**

15. **Descensus frontalis**- No contact below olfactory tracts (0); abutting each other or contacting parabasisphenoid below olfactory tracts (1). **(L7; LCO)**

16. ***Frontal shape**- Long and narrow anteriorly, straight orbital margin (0); broad and rectangular, straight orbital margin (1); long and broad anteriorly, constricted orbital margin (2). **(C6; C9; C0; LC0; L-2)**

The frontal in all dolichosaurs generally resembles an hour-glass in outline, being expanded at both its anterior and posterior ends and pinched at its mid-point, a configuration very similar to modern teiids. The frontal in Scolecophidians resembles that of dolichosaurs, but is much less constricted at its mid-point. The frontal in Pachyrhachis and Haasiophis is relatively long and rectangular in compared to alethinophidian snakes.

17. **Frontal with sagittal crest**- Absent (0); present (1). **(C9; C0)**

A small sagittal crest is observed on the anterior end of the frontal in Coniasaurus. The frontal in Pontosaurus and MSNM V3662 is a broad flat bone with no evidence of a sagittal crest.

18. **Frontoparietal suture**- In dorsal view, simple straight transverse contact (0); in dorsal view, complex curved or interdigitating contact (1). **(LC0)**

The frontoparietal suture in Pontosaurus, Aphanizocnemus, Coniasaurus, and MSNM V3662 is simple and straight. Conversely, Adriosaurus has a more complex M-shaped frontoparietal suture. Lee and Caldwell (2000) coded Adriosaurus with both states; however, Adriosaurus clearly displays state (1). Lee and Caldwell (2000) also coded aigialosaurs with both states; however, this is incorrect as the frontoparietal suture in aigialosaurs is simple and straight (0).

19. ***Parietal, dorsal surface**- Shorter than frontal (0); as long as frontal (1); longer than frontal (2).

The parietal and frontal in Pontosaurus, Adriosaurus, Aphanizocnemus, MSNM V3662, Pachyrhachis, and scolecophidians are approximately the same size. The

parietal in mosasauroids is smaller than the frontal. Haasiophis, Dinilysia, and alethinophidians have very long parietals compared to the frontal length.

20. ***Descensus parietalis-** Absent or weakly developed ridges (0); prominent flanges, not contacting basisphenoid (1); prominent flanges, contacting basisphenoid (2). **(L7; LC0)**

    Pontosaurus, Adriosaurus, and MSNM V3662 all have well developed descending parietal flanges, but the contact with the basisphenoid cannot be determined; dolichosaurs are, therefore, presume to have no contact between the parietal flange and the basisphenoid.

21. **Parietal table and jaw adductor muscles-** Parietal table very wide to moderately wide, jaw adductors restricted entirely to ventral surface or extend only onto lateral margin of dorsal surface of parietal (0); parietal table a narrow sagittal crest, jaw adductors extend over entire dorsal surface of parietal (1). **(L7; LC0)**

    The parietal table of Pontosaurus, Adriosaurus, and MSNM V3662 appears to have the same configuration as alethinophidian snakes, displaying a narrow elongated sagittal crest. The parietal table of Aphanizocnemus is very large and flat.

22. ***Parietal shape-** Broad posteriorly or rectangular (0); narrow posteriorly or triangular (1). **(C9; C0)**

23. **Suspensorial ramus (posterolateral process) of parietal-** Well-developed (0); extremely short or absent (1). **(L7; LC0)**

Pontosaurus has extremely long and narrow suspensorial rami. Alternatively, the suspensorial rami in MSNM V3662 have been greatly reduced and are even covered by the supratemporal.

24. **Parietal (pineal) foramen**- Present (0); absent (1). **(CCK5; L7; C-9; LC0)**
25. **Upper temporal arch**- Complete, upper and lower temporal fenestrae separated (0); incomplete, upper and lower temporal fenestra confluent (1). **(CCK5; L7; LC0)**
26. **Supratemporal**- In superficial position on dorsolateral surface of parietal (0); in deep position on ventrolateral surface of parietal (1). **(LC0)**
27. ***Supratemporal**- Small, confined to parietal ramus (0); large, extending onto parietal table (1). **(L7; LC0)**

    The supratemporal in Pontosaurus is small and sits between the suspensorial rami of the parietal and the squamosal in a typical reptilian fashion. The supratemporal of MSNM V3662, and possibly Adriosaurus, have become enlarged and are resting on top of the parietal table covering the suspensorial rami, very similar to snakes; however, the identification of the supratemporal in Adriosaurus is tentative.
28. **Postorbital and postfrontal**- Single ('postorbitofrontal') element (0); separate ossifications (1). **(CCK5; L7; C-9; LC0; L-2)**

    Pontosaurus clearly shows separate ossifications of the postfrontal and postorbital; this condition is also observed in Dinilysia. Adriosaurus and MSNM V3662 have a fused postorbitalfrontal. In MSNM 3662 the ventral process of the

postorbitalfrontal is a very wide and robust compared to both mosasauroids and snakes.

29. **Postfrontal-** Forked medially, with an anterior process along the frontal and a posterior process along the parietal (0); not forked medially, does not extend a long distance along frontal or parietal (1). **(C-9; LC0; L-2)**
30. **Postorbital ventral process-** Small, forming less than half of posterior orbital margin, postorbital primarily a temporal bone (0); prominent, forming half or more of posterior orbital margin, postorbital primarily an orbital bone (1). **(C-9; LC0)**
31. ***Anteroventral border of orbit-** Formed by jugal (0); formed by maxilla (1). **(C-9)**
32. **Squamosal-** Present (0); absent (1). **(L7; C-9; LC0)**

    The presence of a squamosal in Pachyrhachis is tentative (Lee and Caldwell, 1998; Zaher and Rieppel, 1999) and has, therefore, been conservatively coded as absent. Adriosaurus and Aphanizocnemus are coded as having a squamosal, however, preservation is poor.
33. **Jugal-** Present (0); absent (1). **(LC0; L-2)**

    The jugal in Pontosaurus and MSNM V3662 is a very large and long element creating an expanded orbital region. Although snakes lack a jugal, Pachyrhachis has been scored as having a jugal. Lee and Caldwell (1998) described Pachyrhachis as possessing a jugal that contacts the maxilla anteriorly and the postorbital posteriorly. Conversely, Zaher and Rieppel (1999) believe that the putative jugal is in fact the anterior end of ectopterygoid, broken and displaced

across the posterior end of the maxilla. The jugal is a bone that bounds the orbit ventrally and posteriorly, contacting the maxilla (and lacrimal) anteriorly and the ventral process of the postorbital posteriorly. The ectopterygoid is a laterally placed palatal bone that contacts the maxilla anteriorly and the pterygoid posteriorly. In lizards, the ectopterygoid is obscured in lateral view by the presence of a jugal; however, in snakes, the jugal has been lost and the ectopterygoid forms the posteroventral margin of the orbit. The putative jugal in Pachyrhachis contacts the maxilla anteriorly and the ventral process of the postorbital posteriorly and, therefore, passes both the positional and relational criteria of the test of similarity for a jugal and not an ectopterygoid. The putative jugal in Dinilysia has recently been re-described as a postorbital (Caldwell and Albino, 2002). The postorbital is a bone that contacts both the prefrontal anteriorly and the jugal/maxilla ventrally. Because the putative jugal in Dinilysia contacts the prefrontal and the maxilla its reinterpretation as a postorbital is justified.

34. **Jugal**- Does not extend anteriorly past orbit (0); extends anteriorly past orbit (1). **(L7; LC0)**

35. **Quadrate suspension**- Articulates dorsally with squamosal, supratemporal and opisthotic (0); articulates dorsally with supratemporal, little or no contribution from other elements (1). **(LC0)**

    Although the supratemporal is greatly enlarged in MSNM V3662, the quadrate still articulates with the squamosal and presumably the opisthotic.

36. ***Quadrate**- 'Normal', i.e., without elaborated suprastapedial and infrastapedial processes (0); 'circular' in lateral view, i.e., with enlarged, curved posteroventrally directed suprastapedial process and posterodorsally directed infrastapedial process (1). **(L7; LC0)**

    The quadrate in Pontosaurus, Aphanizocnemus, and MSNM V3662 is comparable to the circular quadrate in mosasauroids. The identification of a preserved quadrate in Eidolosaurus is tentative.

37. **Quadrate**- Tympanic crest directed laterally but a low ridge (0); tympanic crest (outer conch) directed laterally and a well-developed wall (1); distinct tympanic crest absent and external surface of quadrate only weakly concave (2). **(L7; LC0)**

(b) braincase

38. **Length of basal tubera**- Short (0); long (1). **(C6; C9; C0)**

    Pontosaurus displays greatly elongated basal tubera.

39. **Exoccipital separation dorsal to foramen magnum**- Exoccipitals widely separated above foramen magnum (0); exoccipitals with tiny point contact above foramen magnum (1); exoccipitals in extensive median contact above foramen magnum (2). **(L7; L-2)**

    The exoccipitals in Pontosaurus and MSNM V3662 articulate to the lateral margins of the supraoccipital preventing any contact of the exoccipitals above the foramen magnum. The braincase material in Dolichosaurus is too poorly preserved to be coded for this trait.

40. ***Supraoccipital**- Situated ventral or posteroventral to parietal, does not form part of posterior skull roof (0); situated posterior to parietal, forms part of posterior skull roof (1); situated posterodorsal to parietal, forms part of posterior skull roof. **(L7; LC0)**

In snakes the supraoccipital sutures directly to the posterior margin of the parietal and runs underneath the ventral surface of the parietal. In Pontosaurus and MSNM V3662 the supraoccipital rest on top of the posterodorsal surface of the parietal and gradually slopes ventrally. The supraoccipital in Adriosaurus appears to be similar to the snake condition. Although the supraoccipital is not preserved in Dolichosaurus, the parietal displays a pit for the articulation with the supraoccipital suggesting that the supraoccipital formed part of the posterior skull roof.

(c) palate

41. **Vomer**- Anterior or anteromedial to palatine (0); entirely medial to palatine (1). **(L7; LC0)**
42. **Posterior border of opening for Jacobson's organ**- Closed by contact of maxilla and vomer (neochoanate) (0); not closed by bone (palaeochoanate) (1); closed by contact with vomer and septomaxilla (2). **(L7; C-9)**
43. **Palatine**- Sutured or fused with vomer (0); palatine and vomer with mobile contact (1). **(L7; LC0)**

The vomer in Coniasaurus appears to be fused with the palatine forming a single vomeropalatine element. A vomeropalatine has only ever been described in mosasaurs.

44. ***Palatine-maxilla contact**- Palatine sutured to maxilla (0); palatine meets maxilla in a loose joint or does not contact maxilla (1). **(L-2)**

45. **Epipterygoid**- Present (0); absent (1). **(L7; C-9; LC0)**

(d) lower jaw

46. **Intermandibular septum of Meckel's canal**- Subdivision occurs near posterior end of tooth row with well-developed septum (0); subdivision anterior to posterior end of tooth row, intermandibular septum poorly developed (1). **(C-9; LC0)**

47. **Mental foramina on lateral surface of dentary**- Three or more foramina (0); two or fewer foramina (1). **(L7; LC0; L-2)**

Coniasaurus displays four mandibular foramina. There doesn't appear to be any foramina on the dentary of Pontosaurus.

48. **Splenial-angular contact**- Not, or very slightly, exposed in lateral view (0); greatly exposed in lateral view (1). **(L7; LC0)**

49. **Splenial**- Broadly sutured to anteromedial margin of coronoid (0); not sutured to coronoid, but bones in contact (1); widely separate from anteromedial margin of coronoid (2). **(DC3/DP7; L7; LC0; L-2)**

50. **Surangular**- Does not enter articular cotyle (0); enters and forms half the articular cotyle (1); fused with articular, contribution to articular cotyle cannot be determined (2). **(L7; C-9; LC0)**

51. **Surangular-** Does not project far into dentary, dentary not notched posteriorly (0); with long anterior projection that projects into a deep notch in the dentary (1). **(L7)**
52. **Articular-** Separate from both prearticular and surangular (0); fused with prearticular but not surangular (1); fused with prearticular and surangular (2). **(LC0)**

    There is no suture between the articular and prearticular in Pontosaurus, but there is a defined suture for the surangular.
53. **Retroarticular process-** Simple, without medial flange (0); with medial flange (1). **(L7)**

(e) dentition

54. **Marginal teeth-** With sharp carinae (0); without sharp carinae (1). **(C6; C9; C0; LC0)**
55. **Palatine-** Edentulous (0); toothed (1). **(L7; C-9; LC0; L-2)**
56. **Pterygoid-** Edentulous (0); toothed (1). **(CCK5; L7; C-9; LC0; L-2)**

    The pterygoid in Coniasaurus bears small teeth that have a similar crown morphology to the maxillary teeth, slightly thickened with a small, blunted tip. Conversely, the pterygoid in Pontosaurus is smooth and devoid of teeth.
57. **Tooth pedestals-** Absent (0); present, strong and elevated (1). **(C9; LC0)**
58. **Tooth crown inflation-** Not inflated (0); crown moderate to thick inflation [bulbous] (1). **(C9; C0)**

    Tooth crown inflation is a feature only observed in the dentition of Coniasaurus.

(f) axial skeleton

59. **Orientation of zygapophyses of mid-trunk vertebrae-** Steeply inclined medially, 30° or more form the horizontal (0); moderately inclined medially, between 15° and 30° form the horizontal (1); not inclined medially, less than 15° from horizontal (2). **(L-2)**

60. **Neural spines on dorsals-** High spinous projection (0); reduced to low ridges (1). **(L7; LC0)**

61. **Ribs-** Begin from fourth (or more posterior) cervical vertebra (0); begin from third (or more anterior) cervical vertebra (1). **(L7; LC0)**

62. **Lymphapophyses-** No forked free ribs (0); three or more cloacal vertebrae with forked ribs (1). **(L7; L-2)**

63. ***Number of presacral vertebrae-** 27 to 33 (0); 34 to 50 (1); 120 or more (2). **(LC0)**

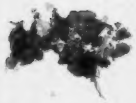
Aigialosaurus has 27 presacrals. Mosasaurs have between 27-42 presacrals. Dolichosaurs have between 34-50 presacrals: Pontosaurus has 40; Adriosaurus has 39; Aphanizocnemus has 35-36; Dolichosaurus has approximately 50; Acteosaurus has 34+; Eidolosaurus has 34; and MSNM V3662 has 35. All snakes have 120 or more.

64. ***Number of cervical vertebrae-** Seven (0); ten to twelve (1) nineteen or more (2). **(LC0)**

Pontosaurus appears to have 12 cervicals. Adriosaurus, Aphanizocnemus, Eidolosaurus, and MSNM V3662 have either 10 or 11 cervicals. Only 8 cervicals are preserved Acteosaurus, but there must have been at least 10 cervicals because

the anterior cervical region and the skull is missing. Dolichosaurus has 19 cervicals.

65. ***Shape of condyles and cotyles in mid-dorsal vertebrae**- Oval, horizontal (mediolateral) dimension wider than vertical (dorsoventral) dimensions (0); circular (1); condyles circular and cotyles oval (2). **(L7; LC0)**



Coniasaurus and Dolichosaurus appear to have a combined morphology; the condyles are circular and the cotyles are constricted into an oval shape. The shape of the condyles and cotyles in the remaining dolichosaurs cannot be determined.

66. **Condyle inclination, dorsal vertebrae**- Inclined (0); vertical (1). **(C6; C9)**

67. **Pachyostosis of mid-dorsal vertebrae and ribs**- Absent (0); present (1). **(LC0)**

Pachyostosis is present in the dolichosaurs Eidolosaurus, Pontosaurus, MSNM V3662, and Adriosaurus, and in the fossil snakes Pachyrhachis and Haasiophis.

68. ***Pygals (anterior caudal vertebrae lacking chevrons)**- Four or more (0); two (1); one (2). **(L7)**

Both aigialosaurs and dolichosaurs are polymorphic for this trait. Aigialosaurus, the Trieste aigialosaur and Adriosaurus have two pygals; Carsosaurus, Aphanizocnemus, Dolichosaurus, and Eidolosaurus all have one pygal.

69. **Caudal transverse processes**- Present on all caudal vertebrae (0); absent in distal caudal vertebrae (1). **(L7)**

70. **Caudal neural spines**- Not taller than dorsal neural spines, tail not dorsoventrally expanded (0); taller than dorsal neural spines, tail dorsovenrally expanded (1). **(L7)**

(g) shoulder girdle and forelimb

71. **Calcified sternum**- Present (0); absent (1). **(L7)**

72. **Scapula-coracoid fusion**- Not fused (0); bones fused (1). **(C6; C9; C0)**

    The scapula-coracoid in Pontosaurus, Aphanizocnemus, and MSNM V3662 is clearly fused. Dolichosaurus and Coniasaurus have a separate scapula and coracoid. This trait is polymorphic for aigialosaurs as the scapula-coracoid in Opetiosaurus is fused and in Haasia is unfused.

73. **Anterior (primary) coracoid emargination**- Present (0); absent (1). **(LC0)**

74. **Epipodials**- Parallel (0); distally diverging (1). **(LC0)**

    The epipodials in Pontosaurus, Adriosaurus, Eidolosaurus, and MSNM V3662 are all greatly distally diverging. Acteosaurus and Aphanizocnemus have parallel epipodials. The condition in Coniasaurus and Dolichosaurus cannot be determined. Aigialosaurs are also polymorphic for this trait. The epipodials in Aigialosaurus and the Trieste aigialosaur are widely diverging; the epipodials in Opetiosaurus and Carsosaurus are somewhat divergent; Haasia has parallel epipodials.

75. **Proximal portion of olecranon**- Present (0); absent (1). **(CCK5; L7)**

76. ***Forelimb**- Approximately the same size as hind limb (0); larger than hind limb (1); smaller than hind limb (2).

    In all dolichosaurs except Aphanizocnemus the forelimbs are smaller than the hind limbs. Aphanizocnemus has a very small tibia creating a shortened hind limb.

77. **Manus/pes-** Shorter than propodial/epipodials (0); as long as propodial/epipodials (1).

(h) pelvis and hind limb

78. **Pelvis-** External to sacral or cloacal ribs (0); internal to sacral or cloacal ribs (1). **(L-2)**

79. **Pubis-** Expanded distally, at symphysial margin (0); not expanded distally (1). **(LC0)**

80. ***Fibula-** Distal end not expanded (0); distal end expanded (1).

The fibula in Adriosaurus, Acteosaurus, and MSNM V3662 is narrow proximally and ends in a mediolaterally expanded boot distally. Although the distal end of the fibula in aigialosaurs is wider than the proximal end it does not display the same degree of expansion seen in these dolichosaurs.

APPENDIX II

Data Matrix

Appendix 2.2 1		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Pontosaurus	1	1	0	0	0	?	1	?	1	0	1	0	1	?	?
2	Adriosaurus	?	1	?	?	?	?	1	?	?	0	?	0	1	?	?
3	Aphanizocnemus	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
4	Dolichosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
5	C. crassidens	?	?	?	?	?	?	1	1	0	0	0	?	?	?	?
6	C. gracilodens	?	?	0	?	?	1	1	1	0	?	?	?	1	1	0
7	Acteosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
8	Eidolosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
9	MSNM V783	1	1	0	0	0	?	1	1	?	?	1	?	1	?	?
10	Aigialosauridae	1	0	1	0	?	?	0	?	0	0	0	1	1	?	?
11	Mosasauridae	1	0	1	0	0	1	0	0	0	0	0	1	1	0	0
12	Pachyrhachis	0	1	0	0	0	?	2	2	1	1	1	0	0	0	?
13	Haasiophis	0	0	0	0	0	?	2	2	?	?	1	0	0	?	?
14	Dinilysia	0	1	0	0	0	1	2	2	1	1	1	0	0	0	0
15	Scolecophidia	0	0	0	1	1	0	2	0	-	-	1	0	0	0	1
16	Alethinophidian	0	0&1	0	1	1	1	2	0&2	1	1	1	0	0	1	1
17	Varanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2.2 2		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1	Pontosaurus	2	0	0	1	1	1	0	0	0	0	0	0	1	0	1
2	Adriosaurus	2	?	1	1	1	1	0	?	0	0	0	1	0	0	1
3	Aphanizocnemus	2	?	0	1	?	0	0	?	?	?	?	?	?	?	?
4	Dolichosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
5	C. crassidens	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
6	C. gracilodens	2	1	0	?	?	?	?	?	?	?	?	?	?	?	?
7	Acteosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
8	Eidolosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
9	MSNM V783	2	0	0	1	1	1	0	1	0	0	0	1	0	0	1
10	Aigialosauridae	0	1	0	0	?	0	1	0	0	0	1	0	0	0	0
11	Mosasauridae	0	1	0&1	0	1	0	1	0	0	0	1	0	0	0	0
12	Pachyrhachis	1	0	1	1	2	1	0	1	1	1	0	1	0	0	1
13	Haasiophis	1	0	1	2	2	1	0	1	1	1	0	1	0	1	1
14	Dinilysia	1	0	1	2	2	1	0	1	1	1	0	1	1	1	0
15	Scolecophidia	2	0	1	1	2	1	0	1	1	1	-	-	-	-	-
16	Alethinophidian	1	0	1	2	2	1	0	1	1	1	0	1	0	0&1	1
17	Varanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2.2 3		31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
1	Pontosaurus	0	0	0	0	0	1	1	1	0	2	?	?	?	?	0
2	Adriosaurus	0	0	0	?	?	?	?	?	?	1	?	?	?	?	0
3	Aphanizocnemus	0	0	0	0	?	1	?	?	?	?	?	?	?	?	?
4	Dolichosaurus	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?
5	C. crassidens	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?
6	C. gracilodens	?	?	?	?	?	?	?	?	?	?	0	1	0	0	?
7	Acteosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
8	Eidolosaurus	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
9	MSNM V783	0	0	0	0	0	1	1	?	0	2	?	?	?	?	?
10	Aigialosauridae	0	0	0	1	0	1	1	1	?	0	?	?	?	?	0
11	Mosasauridae	0	0	0	1	0	1	1	1	0	0	0	1	0	0	0
12	Pachyrhachis	1	1	0	0	1	0	2	0	0	1	1	?	1	?	1
13	Haasiophis	1	1	1	-	1	0	2	0	0	1	1	?	1	1	1
14	Dinilysia	1	1	1	-	1	0	2	0	1	1	0	2	1	1	1
15	Scolecophidia	-	1	1	-	-	0	2	0	1	1	0	2	1	1	1
16	Alethinophidian	1	1	1	-	1	0	2	0	1	1	1	2	1	1	1
17	Varanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2.2 4		46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
1	Pontosaurus	?	1	1	1	1	0	1	1	1	?	0	1	0	?	?
2	Adriosaurus	?	?	?	?	0	?	?	1	?	?	?	?	0	?	1
3	Aphanizocnemus	?	?	?	?	?	?	?	?	1	?	?	?	0	0	1
4	Dolichosaurus	?	?	1	?	?	0	?	?	?	?	?	?	?	2	1
5	C. crassidens	0	0	1	1	?	0	?	?	1	?	?	0	1	0	1
6	C. gracilodens	?	?	?	?	?	?	?	?	1	0	1	0	1	0	1
7	Acteosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
8	Eidolosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
9	MSNM V783	?	?	?	?	?	?	?	1	?	?	?	?	0	?	1
10	Aigialosauridae	?	?	1	1	1	0	1	1	0	0	?	1	0	0	0
11	Mosasauridae	0	0	1	2	1	0	1	1	0	0	1	1	0	0	0
12	Pachyrhachis	?	1	0	?	2	1	2	-	0	1	1	0	0	1	0
13	Haasiophis	?	1	0	?	2	1	2	0	?	1	1	0	0	?	?
14	Dinilysia	1	1	0	2	2	1	2	0	?	?	1	0	0	1	1
15	Scolecophidia	1	1	0	0	2	1	2	0	0	0	0	0	0	1	1
16	Alethinophidian	1	1	0	2	2	1	2	0	0	1	1	0	0	1&2	1
17	Varanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2.2 5		61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
1	Pontosaurus	0	0	1	1	?	?	1	?	?	?	1	1	0	1	0
2	Adriosaurus	1	0	1	1	?	1	1	1	1	1	0	?	?	1	1
3	Aphanizocnemus	0	0	1	1	?	?	0	2	1	1	1	1	0	0	1
4	Dolichosaurus	0	0	1	2	2	0	0	2	1	1	0	0	1	0	?
5	C. crassidens	?	?	?	?	2	0	0	?	?	?	?	?	?	?	?
6	C. gracilodens	?	?	?	?	2	0	0	?	?	?	?	0	1	?	?
7	Acteosaurus	?	0	1	1	?	?	0	?	1	1	?	?	?	0	1
8	Eidolosaurus	0	0	1	1	?	?	1	2	1	1	?	?	?	1	0
9	MSNM V783	1	0	1	1	?	?	1	0	1	1	?	1	0	1	?
10	Aigialosauridae	1	0	0	0	0	0	0	1&2	1	1	0	0&1	0&1	0&1	0
11	Mosasauridae	1	0	0&1	0	1	1	0	0	1	1	0	0	0&1	0&1	1
12	Pachyrhachis	1	0	2	2	?	?	1	-	?	0	-	-	-	-	-
13	Haasiophis	?	1	2	2	?	?	1	-	?	?	-	-	-	-	-
14	Dinilysia	?	?	2	2	1	?	0	-	?	?	-	-	-	-	-
15	Scolecophidia	1	1	2	2	0	?	0	-	0	0	-	-	-	-	-
16	Alethinophidian	1	1	2	2	1	?	0	-	0	0	-	-	-	-	-
17	Varanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2.2 6		76	77	78	79	80
1	Pontosaurus	?	1	?	?	?
2	Adriosaurus	2	1	0	1	1
3	Aphanizocnemus	1	1	0	1	0
4	Dolichosaurus	?	?	0	?	?
5	C. crassidens	?	?	?	?	?
6	C. gracilodens	?	?	?	?	?
7	Acteosaurus	2	1	0	?	1
8	Eidolosaurus	2	1	0	?	?
9	MSNM V783	2	1	0	?	1
10	Aigialosauridae	0	0	0	0	0
11	Mosasauridae	1	1	0	0	0
12	Pachyrhachis	-	-	0	1	0
13	Haasiophis	-	-	1	?	?
14	Dinilysia	-	-	?	?	?
15	Scolecophidia	-	-	1	-	-
16	Alethinophidian	-	-	1	-	-
17	Varanus	-	0	0	0	0

CHAPTER THREE

DOLICHOSAUR PALEOECOLOGY

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INTRODUCTION

The origin of snakes is undoubtedly one of the most interesting episodes in vertebrate history. This dramatic evolutionary event combined a major shift in habitat with the appearance of new structural-functional complexes. Over the last century, researchers have been trying to examine the origin and evolution of these unique animals, but little consensus has been achieved (see Rieppel, 1988 for historical review; Lee, 1997; 1998; Caldwell and Lee, 1997; Lee and Caldwell, 1998; 2000; Zaher, 1998; Caldwell, 1999a; Zaher and Rieppel, 1999; 2000; Rieppel and Zaher, 2000; Tchernov et al., 2000). Recently, however, several phylogenetic analyses have found dolichosaurs to be the sister group to snakes (Lee and Caldwell, 2000; Pierce and Caldwell, 2002; Chapter 2). Additionally, these studies have revealed that dolichosaurs are a non-monophyletic assemblage. Therefore, for the purpose of the current study, the term dolichosaur will be used in the paraphyletic sense to refer to all elongate, limb-reduced, Upper Cretaceous marine squamates.

Because dolichosaurs occupy a potentially crucial phylogenetic position to snakes, it is important to recognize aspects of their paleoecology as a means of understanding the paleoecology of snake origins. The logic behind such comparisons is based on the idea that if snakes and dolichosaurs are successive sister taxa then they must share some features of their common ancestor. Marine adaptations might well be on this list.

Original descriptions and discussions (Owen, 1850; Meyer, 1860; Kornhuber, 1873; Seeley, 1881; Kramberger, 1892; Nopcsa, 1903; 1908; 1923) did not examine dolichosaur paleoecology beyond mentioning that the animals were probably aquatic.

Recent descriptive studies of these animals have concentrated on their anatomy and phylogeny (Dal Sasso and Pinna, 1997; Dal Sasso and Renesto, 1999; Caldwell, 1999b; 2000; Caldwell and Cooper, 1999; Lee and Caldwell, 2000; 2002; Pierce and Caldwell, 2002; Chapter 2), though some preliminary remarks about the mode of life and functional morphology of dolichosaurs have been made (Caldwell, 1999b; 2000; Caldwell and Cooper, 1999; Lee and Caldwell, 2000). Here these interpretations are modified and extended in light of a new understanding of dolichosaur morphology and phylogeny.

GENERAL APPROACH TO STUDY

This study is composed of two primary sections, geology and paleobiology. In the geology section, the habitat and distribution of dolichosaurs are discussed. A detailed description of the stratigraphy and depositional setting of dolichosaur fossils is given in order to create a general paleoenvironmental interpretation and to arrive at some paleobiogeographical conclusions. In the paleobiology section, dolichosaurs are examined within four broad categories: body structure, locomotion, terrestrial behaviour, and feeding and foraging. A variety of fossil (e.g., mosasaurs and pachyophiids) and modern (e.g., sea snakes) analogues are utilized.

GEOLOGY

Stratigraphical and Depositional Setting

1. Anglo-Paris Basin

The Anglo-Paris Basin was a west-east trending depression in Western Europe, extending from Ireland to Germany, which was submerged by the transgression of the

Tethys Seaway and the Northern Atlantic during the Upper Cretaceous (Fig. 3-1). The basin supported an extensive continental shelf that was relatively flat and featureless. Coalescence of warm waters from the Tethys and cool waters from the Atlantic combined to produce a somewhat temperate environment. Sedimentary deposits in the basin are largely marine carbonates that are characterized by massive chalks alternating with thinner marl units.

1.1 England

Locality and Stratigraphy—Coniasaurus and Dolichosaurus remains have been described from the Lower Chalk (Cenomanian) of North and South Downs in southeast England (Caldwell and Cooper, 1999; Caldwell 1999b, 2000) (Fig. 3-2). Collection data are insufficient to allow accurate placement of most specimens to a specific formation, member, or horizon; however, some specimens have been placed in the Chalk Marl Formation (Lower-Middle Cenomanian), the Abbott's Cliff or Grey Chalk Formation (Upper Cenomanian), and the Plenus Marl Horizon (Upper Cenomanian). On the whole, the collection data does indicate a pit or outcrop, closest town or village, and the county or provenance. Coniasaurus remains have been recovered from: Peter's Pit, Wouldham, Kent; Blue Bell Hill, Burham, Kent; Hart Hill, Charing, Kent; Clayton Chalk Pit, near Brighton, East Sussex; Lidden Spout, near Folkestone, East Sussex; and Washington, near Worthing, West Sussex. Dolichosaurus remains have been recovered from: Southerham Pit, near Lewes, Sussex, and Burham, Kent.

Lithology and Sedimentology—The Lower Chalk is composed primarily of a massive soft chalk deposit. The chalk is white, relatively pure, and intensely bioturbated.

The Lower Chalk is divided into bands and beds of glauconitic sands, marls, compact lithified chalks, and calcaranitic chalks with abundant shell material. Flints are also found scattered throughout the unit (Robinson, 1986; Owen, 1987).

Fauna and Flora—The fauna of the Chalk is extremely diverse and has been well documented. Sponges, byozoans, brachiopods, bivalves, gastropods, ammonites, belemnites, arthropods, and echinoderms have all been described. Remains of fish and shark teeth and scales are widely distributed. Reptile remains are also common and include, plesiosaurs, pliosaurs, dinosaurs, and pterosaurs (Owen, 1987).

Depositional Setting—The Lower Chalk is interpreted as a shallow marine deposit that formed on a broad open shelf. Deposition occurred at water depths less than 50m and up to 300m (i.e., offshore). Soft chalks appear to have formed in a relatively deep-water setting; the glauconitic sands, marls, compact chalks, and calcaranitic chalks are thought to have formed in a fairly shallow shelf environment (i.e., foreshore) and may even indicate periods of sub-aerial exposure (Hattin, 1975). The majority of dolichosaur fossils come from marl units and were, therefore, deposited in relatively shallow water.

1.2 Germany

Locality and Stratigraphy—Fragments of Coniasaurus and Dolichosaurus have been uncovered in Halle/Westphalia, NW Germany (Diedrich, 1997,1999) (Fig. 3-2). The specimens were found amongst large ammonite scour troughs in the Blackcoloured Formation (Upper Cenomanian) of the Teutoburger Wald. Specifically, the specimens come from the 'scour trough horizon I' of the Puzosia-Event I.

Lithology and Sedimentology—The Blackcoloured Formation is divided into a lower carbonate complex, a middle black shale complex, and an upper green-grey marl complex. The Puzosia-Event I is an ammonite scour trough system that is preserved in the lower carbonate complex in an extensive chalk deposit (Diedrich, 1997, 1999, and web site).

Fauna and Flora—Besides preserving exceedingly large ammonites, the Blackcoloured Formation is characterized by a diverse fossil assemblage. Bivalves, gastropods, annelids, crustaceans, bryozoans, brachiopods and echinoderms comprise the invertebrate fauna. The majority of vertebrate fossils are sharks, however, abundant fish remains are also present. Out of 251 macrofaunal remains in scour trough horizon I, 62% are inoceramid bivalves (Diedrich, 1997, 1999, and web site).

Depositional Setting—The carbonate complex of the Blackcoloured Formation is a pure marine deposit. The Puzosia-Event I formed in a deep, flat shelf environment at depths around 150-200m (i.e., offshore). Based on the fragmentary nature of the dolichosaur specimens it has been suggested that the carcasses are not in situ; instead, the animals may have been transported into the open sea from a shallower water environment and trapped by the large ammonite scour troughs (Diedrich, web site).

2. Northern Tethys Region

During the Upper-Cretaceous (Albian-Turonian), landmasses of what are now known as the Mediterranean region, northeastern Africa, the Middle East, and the previous southwestern border of the Soviet Union were submerged during a major transgressive phase of the Tethys Seaway (Fig. 3-1). The shallow flooded continental

margins formed extensive carbonate platforms that supported the development of widespread patch-reefs and inter-platform basins/lagoons (Follmi, 1989). To the west of the Middle East, along Africa's northeastern border, there was an extensive barrier reef system (Scanlon et al., 1999; Caldwell and Albino, 2001). Sedimentary deposits in the region are largely marine carbonates. Depending on the proximity to a terrigenous body, there can be varying amounts of clastic sediments.

2.1 Slovenia

Locality and Stratigraphy— Adriosaurus and Acteosaurus were both discovered in Komen, Slovenia, in the Karst of Trieste or the Trieste-Komen Plateau (Meyer, 1860; Seeley, 1881; Calligaris, 1993; Lee and Caldwell, 2000) (Fig. 3-2). Unfortunately, the formation and specific localities where the specimens were found have not been documented; however, the specimens do come from platy limestone blocks that are assumed to be of Lower to Middle Cenomanian age (Langer, 1961; Gušić et al., 1988). Therefore, the fossils are probably preserved in the Pivor Formation (Jurkovšek et al., 1996)

Lithology and Sedimentology—The Komen Limestone (Pivor Formation) is a thin-bedded, platy, and laminated limestone. It is a bituminous, dark grey or black mudstone to wackestone (Jurkovšek et al., 1996). It is locally intercalated by laminae of calcareous slates and contains both chert nodules and chert sheets (Ogorelec et al., 1987; Kolar-Jurkovšek et al., 1996). Layers of stromatolite and flat pebble conglomerate are also apparent throughout the unit (Ogorelec et al., 1996; Cavin et al., 2000). The Komen Limestone is overlain and surrounded by rudistic limestones (Ogorelec et al., 1987).

Fauna and Flora—The Komen Limestone is fossiliferous. It is well known for its exceptionally preserved fossil fishes (Cavin et al., 2000). Aquatic reptiles, including aigialosaurs, and pachyophiids are present. Ammonites, echinoderms, ostracods, rudists, oysters and 'non-skeletal' algae are abundant throughout the unit. In addition, plant debris is dispersed throughout the section (Kolar-Jurkovšek et al., 1996; Summesberger et al., 1996).

Depositional Setting—The Komen Limestone is a typical shallow water marine deposit. Deposition is believed to have occurred on a very shallow, highly restricted inner shelf. The shelf area is thought to have been between the foreshore to very shallow shoreface zone of a tidal flat. Inter-platform basins/lagoons were a predominate feature of the tidal flat and would have been surrounded by abundant rudist-dominated reefs (Ogorelec et al., 1987 and 1996; Gušić et al., 1988; Jurkovšek et al., 1996; Cavin et al., 2000).

2.2 Croatia

Locality and Stratigraphy—Pontosaurus, Eidolosaurus, and another specimen of Adriosaurus were collected from Hvar Island (=Isola di Lesina), Croatia (Kornhuber, 1873; Nopcsa, 1923; Calligaris, 1993; Lee and Caldwell, 2000; Pierce and Caldwell, 2002) (Fig. 3-2). Unfortunately, the formation and specific localities where the specimens were found have not been documented. The specimens do, however, come from platy limestone blocks that are assumed to be of Lower to Middle Cenomanian age (Langer, 1961; Gušić et al., 1988). Therefore, the fossils were probably found in either

the Vidova Gora Formation (Gušić et al., 1988) or the Milna Formation (Gušić and Jelaska, 1990; Tešović et al., 2001).

Lithology and Sedimentology—The platy, very fine-grained, limestones on Hvar Island (Vidova Gora Formation or Milna Formation) are composed of three superpositional units. The lower part consists of alternating limestones of various subfacies, the middle of a thick dolomite sequence, and the upper part of laminite slabs alternating with muddy mounds, skeletal limestones, stromatolitic limestones, and flat-pebbled conglomerates. The rocks from the upper part also reveal desiccation cracks and red coloured upper bedding planes (Hemleben and Freels, 1977; Gušić et al., 1988; Gušić and Jelaska, 1990).

The slab of rock that Pontosaurus is preserved on is a very fine-grained and thinly laminated biomicritic limestone. In thin section, the rock has alternating thick light and thin dark layers. The light layers are 100% bioturbated while the dark layers are organically rich with abundant fecal pellets and are not laterally uniform. Stylolites are also present throughout the rock and the upper bedding plans are red in colour (pers. com. with A. Kaswani). Based on these characteristics, Pontosaurus probably comes from the upper part of the platy limestones.

Fauna and Flora—Hvar Island preserves a diverse fish assemblage (Radovčić, 1971; Bardack and Radovčić, 1972). Aquatic squamates including aigialosaurs are exceptionally preserved. Abundant remains of rudists, oysters, inoceramids, gastropods, ammonites, squid, starfish, crustaceans, ostracods, and cyanobacterial mats are present throughout the unit (Bardack and Radovcic, 1972; Mamužić et al., 1979; Babinot, 1988; Gušić and Jelaska, 1990; Moro, 1997). Dinosaur footprints and several species of plants

have also been identified and analyzed (Bardack and Radovcic, 1972; Mezga and Bajraktarević, 1999).

Depositional Setting—Deposition of the platy limestones on Hvar Island occurred under highly restricted conditions, typical of an inner or protected platform environment. Sedimentation took place in the foreshore to very shallow shoreface. The tidal flats were large and supported extensive cyanobacterial mats. In particular, deposition on Hvar Island happened in shallow (5-10m) inter-platform basins/lagoons amidst growing rudists reefs (Radovcic, 1971; Hemleben and Freels, 1977; Mamuzic et al., 1979; Gusic et al., 1988; Gusic and Jelaska, 1990).

2.3 Lebanon

Locality and Stratigraphy—Aphanizocnemus was discovered in the Upper Cretaceous (Lower Cenomanian-Middle Cenomanian) of Lebanon (Dal Sasso and Pinna, 1997; Dal Sasso and Renesto, 1999) (Fig. 3-2). An exact locality is unknown, however, the specimen was collected from limestone beds along with a variety of fish fossils from one of the sites of Hakel, Hadjula, and Nammoura about 40km NE of Beirut. Another, unidentified, dolichosaur specimen (MSNM V3662) is also known from Lebanon (Dal Sasso and Renesto, 1999) (Fig. 2). This second specimen comes from Nammoura. The limestone outcrops in Hakel, Hadjula, and Nammoura all belong to the Sannine Formation ('Fish Beds') and are Cenomanian in age (Walley, web site).

Lithology and Sedimentology—The Sannine Formation is composed of thinly laminated limestones alternating with more massive limestones. Occasional nodules and lenses of impure chert occur throughout the unit. The fossil lizards are preserved on very

compact, flinty lithographic slabs of limestone. The rock is grey-yellowish in colour with fine, parallel lamination and is not bioturbated (Dal Sasso and Pinna, 1997). The Sannine Formation is overlain by thick rudist bank deposits (Patterson, 1967; Krassilov et al., 2000).

Fauna and Flora—Medium to large size fish remains are the main constituents of the world renowned 'Fish Beds' of Lebanon. However, the 'Fish Beds' also exhibit a diverse faunal and floral assemblage. Aquatic squamates such as limbed snakes are present (Rage and Escuillié, 2000) and the limb bone of a theropod dinosaur has even been discovered. Crustaceans, bivalves and plant remains are also abundant throughout the section. (Dal Sasso and Renesto, 1999; Krassilov et al., 2000).

Depositional Setting—The Sannine Formation was deposited in a shallow water marine environment. It is hypothesized that the limestones are platform carbonates formed during regular and constant periodical sedimentary episodes in a low-energy depositional environment (Dal Sasso and Pinna, 1997). Specifically, the fossiliferous beds are thought to have been laid down in an inter-platform basin/lagoon setting between rudist-dominated patch reefs (Hückel, 1970; 1974; Scanlon et al., 1999).

2.4 Kazakhstan

Locality and Stratigraphy—An isolated dolichosaurian vertebra has been recently described from Kazakhstan (Averianov, 2001) (Fig. 3-2). The species remains indeterminate. The vertebra was discovered in the upper phosphatic horizon (Cenomanian) in the Besokty II locality in the southern part of the Mangyshlak Plateau.

Lithology and Sedimentology—The Cenomanian of the Mangyshlak Plateau is comprised of sands, silts, marls, and thin phosphatic conglomerates. The conglomerates have a sandy matrix that is locally glauconitic and fall into two categories: structureless, bioturbated sands that commonly contain silt and a little clay, and thin trough-cross laminated units that represent storm events. The silty marls contain abundant infilled burrows (Marcinowski and Walaszczyk, 1996; Gale et al., 1999).

Fauna and Flora—The invertebrate fauna in the Mangyshlak Plateau is diverse and includes: ammonites, belemnites, gastropods, irregular echinoids, and inoceramid bivalves. The vertebrate assemblage consists almost entirely of sharks (Marcinowski and Walaszczyk, 1996; Averianov, 2001).

Depositional Setting—Deposition of the Cenomanian rocks in the Mangyshlak Plateau was in a shallow marine setting (Kopaevich and Walasczyk, 1990; Gale et al., 1999). Sedimentation is believed to have occurred on the continental shelf with fairly large input of fine terrigenous sediments. Specifically, it has been suggested that the depositional environment was a muddy outer submarine fan that had regular sandy spells and phosphatic condensation horizons (Gaetani et al., 1998).

3. Western Interior Basin

The Western Interior Basin of North America evolved as a complex foreland basin between the Jurassic and Cretaceous in response to accelerated plate spreading, convergence, and subduction along the western margin of North America (Fig. 3-1). Westward translation of compressive forces episodically deformed this basin and divided it into three broad structural provinces: (1) a western zone of plutonism, volcanism, and

thrusting–the Cordilleran thrust belt; (2) a foreland basin; and (3) a broad, shallow, eastern epicontinental shelf (Kauffman, 1985). The Western Interior Basin became flooded by shallow epicontinental seas from both the North (Boreal; Cool Temperate) and South (Caribbean; Warm Temperate to Subtropical) beginning in the Barremian-Middle Albian time (Kauffman 1985). Initial connection of the northern and southern arms of the seaway took place in the Late Albian with the junction of the Skull Creek Sea from the north and the Kiowa Sea from the south. The seaway remained joined for 38 Ma until the Middle Maastrichtian (Kauffman, 1977; 1985; Gustason and Kauffman, 1984).

The sedimentological record of the Western Interior Basin reflects the dynamic structure of the basin. Along the western margin of the seaway there are thick sequences of coarse, continental, marginal-marine, and near shore marine terrigenous sediments. In the deep, west-central part of the basin, sediments are characterized by dark silty clay and calcareous clay-shales, intercalated with thinner distal (basinal) extensions of pelagic carbonate units from the eastern shelf and sand-dominated facies from the west. The eastern platform zone is dominated by clayey, silty, and calcareous shales, and by abundant pelagic carbonates deposited in shallow (photic) waters (Kauffman, 1985).

3.1 United States

Locality and Stratigraphy—Numerous dolichosaur remains, assigned to the species Coniasaurus crassidens, have been uncovered from sediments deposited in the North American Western Interior Basin (Bell et al., 1982; Bell, 1993; Bell and Polcyn, 1996; Cicimurri and Bell, 1996; VonLoh and Bell, 1998) (Fig. 3-2). Specifically,

Coniasaurus specimens have been discovered in the Greenhorn Formation (Orman Lake Member; Upper Cenomanian) and the Carlile Shale (Turner Sandy Member; Upper Turonian) of South Dakota. They have also been found in the Greenhorn Limestone (Upper Cenomanian) of Kansas. Additional specimens have been described from the Lake Waco Formation (Bluebonnet Member; Upper Cenomanian), the Boquillas Formation (Ernst Member; Lower-Middle Turonian), the Britton Formation (Upper Cenomanian), and the Arcadia Park Formation (Upper Turonian) of the Texas Gulf Coast.

3.1.1 Greenhorn Formation/Limestone

Lithology and Sedimentology—The Greenhorn Formation/Limestone is composed predominantly of dark coloured, marls to the south and east, and clay rich shales to the west (MacDonald, 1984). Specifically, the Orman Lake Member is composed primarily of marl and calcareous shale, throughout which occur thin lenses and beds of skeletal limestones, bentonite seams, and zones of concretionary carbonate (Foell, 1982).

Fauna and Flora—The Greenhorn Formation/Limestone has a diverse faunal assemblage. Fish and shark fragments, including teeth, scales, ribs and other bones, are common. Remains of plesiosaurs, pliosaurs, mosasaurs and even a pterosaur have been documented (VonLoh and Bell, 1998). A variety of ammonites and bivalves are also present. Inoceramid bivalves are the most common fossils in the unit (Foell, 1982).

Depositional Setting—Deposition of the Greenhorn Formation/Limestone is thought to have occurred in the outermost parts of the stable eastern carbonate shelf

(Hattin, 1975; Foell, 1982; MacDonald, 1984). Clastic input was derived from the western margin of the seaway (Foell, 1982). Carbonate rich facies of the Greenhorn Formation/Limestone were deposited at depths shallower than the clayey shales. On the basis of sedimentary structures and faunal assemblages, it is estimated that the carbonate-rich sediments were deposited on a shallow carbonate platform in minimum depths of 20-35 meters (i.e., shoreface) and maximum depths of 61-150 meters (i.e., offshore) (Kauffman, 1969; Foell, 1982).

3.1.2 Carlile Formation

Lithology and Sedimentology—The Turner Sandy Member of the Carlile Formation is generally composed of interbedded, light olive to dark grey sandstones and greyish-black siltstones. More specifically, the member is characterized by three distinct sedimentary units: (lower) very silty, thin, fine-grained sandstone beds, separated by shale partings; (middle) medium-grained, bioturbated calcareous sandstones; and (upper) very fine-grained, non-calcareous sandstones that contain significant amounts of clay and silt (Galperin, 1998). The Turner Sandy Member sandstones are well sorted and display ripples, megaripples, and low-and high-angle cross-stratification (Leite et al, 1988; Pinel, 1977; Galperin, 1998).

Fauna and Flora—The Turner Sandy Member is nearly devoid of well-preserved fossils, however, fragments of a variety of organisms have been described. There is an abundance of shark and fish teeth and scales found throughout the unit (Leite et al., 1988; Hattin, 1962). The invertebrate fauna includes annelid burrows, inoceramids, and cephalopods (Hattin, 1962).

Depositional Setting—The Turner Sandy Member of the Carlile Formation was deposited in a very shallow environment along the shoreline of the eastern carbonate shelf. The lower bed was deposited in a transitional zone between fair-weather and storm wave base. Sediments were deposited during conditions of alternating storm surges and periods of low slack-water deposition; such conditions are consistent with a transitional zone from the offshore to the shoreface. The middle unit is a product of a high-energy environment, typical of the shoreface and foreshore. In general the middle unit represents a barrier island complex; behind the barrier islands, development of lagoons occurred. The upper component of the Turner Sandy Member was deposited on the foreshore and is characterized by the seaward progression of the lagoons (Pinel, 1977; Galperin, 1998).

3.1.3 Lake Waco Formation

Lithology and Sedimentology—The Bluebonnet Member of the Lake Waco Formation consists of a sequence of limestones, shales and bentonite beds. Limestone beds dominate the section and are lenticular in shape in the basal layers and become fairly uniform and horizontal in the upper layers. Shale beds are grey, fissile, thinly laminated, and calcareous. Current action is indicated by cross bedding within strata, lenticular beds, current ripple marks, and fragmentary shell material (Chamness, 1963; Silver, 1963).

Fauna and Flora—The lower stratum of the Bluebonnet Member contains a varied and profuse fauna and flora. Fossils are more commonly found in the lenticular limestones and shales. Fish scales and teeth are common, along with plesiosaurs and

mosasaurs. Invertebrates are predominantly benthic pelycopods, ammonites, and gastropods. Inoceramid bivalves are the most common fossils in the unit (Chamness, 1963; Silver, 1963). Plant material and coal are also common throughout the member. Impressions of stems up to six inches in diameter have been described. The plant material appears to be the remnants of marsh-growing reeds (Chamness, 1963).

Depositional Setting—The Bluebonnet Member of the Lack Waco Formation is interpreted as a shallow restricted embayment or lagoonal deposit on the proximal eastern shelf. The lenticular limestones of the basal layers probably developed from a calcareous sand deposit along a foreshore zone or bar. A more widespread environment appears to have existed during later deposition as indicated by horizontal bedding. Carbonaceous plant debris and plant impressions in the basal Bluebonnet Member suggest a brief period in which coastal swamps might have developed (Chamness, 1963; Silver, 1963).

3.1.4 Boquillas Formation

Lithology and Sedimentology—The Ernst Member of the Boquillas Formation is composed of alternating layers of laminated black calcareous shales and limestones. The lower part of the unit is a thinly laminated limestone rich in skeletal grains. It is intercalated with calcareous shales and bentonite seams. Hummocky cross-stratification and sand-filled channels characterize these limestones. The upper part of the unit is horizontally laminated, fine-grained, black calcareous shales, limestones, and marls. They are bioturbated and are intercalated with phosphatic horizons, sandy zones, and calcarenites (Sanders, 1988; Trevino, 1988). The fossil lizards are preserved in the calcarenites of the upper part of the Ernst Member (Cicimurri and Bell, 1996).

Fauna and Flora—Sharks' teeth are the most common fossils in the Ernst Member. There is also an abundance of fish teeth, scales, and bones. Rare aquatic reptiles including mosasaurs and pliosaurs have been described. Invertebrate fossils consist of ammonites, inoceramids, oysters, and echinoderms (Cicimurri and Bell, 1996; Sanders, 1988; Trevino, 1988).

Depositional Setting—The Ernst Member of the Boquillas Formation was deposited in the shallow pelagic waters of the eastern carbonate shelf. The lowest part of the member was deposited in a high-energy shallow water environment typical of the shoreface. The upper part of the member was deposited in quieter, slightly deeper water of the middle to outer shelf (i.e., offshore). Lagoons and bays characterized the outer portion of the shelf. Deposition of the Ernst Member was in water that ranged from 50m to 150m (Sanders, 1988; Trevino, 1988).

3.1.5 Britton/Arcadia Park Formation

Lithology and Sedimentation—The Britton Formation consists of dark brown laminar calcareous mudstones interbedded with thin, impure beds of limestone, siltstones, and sandstones. The Arcadia Park Formation is composed of grey to dark grey, fissile, calcareous mudstones with thin laminae of siltstones, sandstones, and fragmental limestones. Widespread distribution of both calcareous and terrigenous sediments, often overlapping, suggests interfingering of carbonate and sand depositional environments during Britton/Arcadia Park time. Carbonate bodies include calcareous mudstones, calcareous bioclastic mudstones, packstones, and bioclastic grainstones, all of which indicate wide varieties of carbonate depositional environments (Surles, 1987).

Fauna and Flora—Other than the mention of Coniasaurus remains, there has been no documentation of the fauna and flora from the Britton or Arcadia Park formations.

Depositional Setting—The Britton and Arcadia Park formations were deposited on a delta-dominated shallow marine environment on the proximal eastern shelf. Marine conditions allowed for extensive limestone deposition to occur. Clastic influx was created by prograding, mud-dominated deltas. The distribution of sand throughout the formation is attributed to progradation of the deltas across the shallow marine shelf within extremely quiet water (i.e., shoreface-offshore). Limestone deposition existed in both the interdistributary areas of the deltas and as carbonate banks in marginal embayments around the deltas (Surles, 1987).

PALEOENVIRONMENT AND PALEOBIOGEOGRAPHY

1. Paleoenvironmental Interpretation

Dolichosaur fossil remains are found in a wide variety of depositional environments. Their habitat ranged from tropical waters in the Northern Tethys Region, to subtropical waters in the southern United States, and into the temperate waters of the Anglo-Paris Basin and the mid-west of the United States. Dolichosaurs appear to have inhabited an array of epicontinental marine environments that extended from shallow marginal marine areas inundated with extensive tidal flats, lagoons, and coastal swamps, through shallow offshore patch reefs and inter-platform basins, and into the relatively deep water of the open outer shelf. It appears as though dolichosaurs spent the majority

of their time in free-swimming situations; however, the depositional settings of their fossil remains also suggests they spent time on or near land.

2. Paleogeographical Distribution

Dolichosaur fossil remains are recognized throughout the Cenomanian of Western Europe, Central Asia, the Mediterranean, and the Middle East. They are also known from the Upper Cenomanian to the Upper Turonian of the mid-west and southern United States (Fig. 3-2). Globally, their earliest record is from the Lower-Middle Cenomanian of Slovenia, Croatia, and Lebanon from rocks deposited in the Northern Tethys Seaway. The latest occurrence is from the Upper Turonian of South Dakota and the Texas Gulf Coast from rocks deposited in the North American Western Interior Seaway.

3. Pattern Of Dispersal

The paleobiogeographic pattern of marine organisms during the Cenomanian-Turonian is thought to be a consequence of the circum-global currents within the Tethys Seaway and the widening Atlantic Ocean, both of which contributed to what is known as the Caribbean SuperTethys (Caldwell and Cooper, 1999). A unidirectional westward flow of the Tethy-SuperTethys (Fig. 3-1) is documented in the paleontological record by the paleobiogeographical distribution of invertebrate fauna, such as rudist bivalves (Johnson and Kauffman, 1990; Kauffman and Fagerstrom, 1993).

The dispersal of bivalve larvae is highly dependant on the strength and direction of the prevailing water currents into which the larvae are deposited (Caldwell and Cooper, 1999). Rudist bivalves are believed to have originated in the Berriasian to

Valanginian (Lower Cretaceous) of the European Tethys Seaway. These opportunistic, reef building, bivalves are not recorded from the Caribbean SuperTethys Seaway until the Barremian, roughly 10-12 Mya after their European origin (Johnson and Kauffman, 1990; Kauffman and Fagerstrom, 1993). The pattern of dispersal of rudist bivalves is thought have followed the dominant westward flowing current of the Tethys-SuperTethys as abundant carbonate platforms (reef building niches) developed during periods of eustastic sea level rise (Caldwell and Cooper, 1999).

The paleobiogeographical distribution recognized for dolichosaurs throughout the Cenomanian–Turonian is similar to that observed for bivalves (Caldwell and Cooper, 1999). The earliest appearance of dolichosaur fossils occurs within the Lower-Middle Cenomanian of the Northern Tethys Seaway; it is not until the Upper Cenomanian that dolichosaurs begin to inhabit the North American Western Interior Seaway. This paleobiogeographical pattern suggests that dolichosaurs might have originated in the Tethys Seaway and diversified and dispersed throughout the Cenomanian following the prevailing westward flow of the Tethys-SuperTethys Seaway.

4. Migration Route

Stratigraphical and paleobiogeographical data indicate that dolichosaurs originated in the Tethys Seaway and migrated west into the Western Interior Basin. There are two potential migration routes these small marine squamates could have exploited. The first scenario is that migration was accomplished by following the paleocoastlines of western Africa to South America and then north, along the coastline of numerous small Baltic islands to the coast of southern North America (Caldwell and

Cooper, 1999) (Fig. 3-1). This hypothesis is consistent with the one proposed for the distribution of mosasaurs (Caldwell and Bell, 1994). The second scenario is that dolichosaurs transversed the Northern Atlantic from Western Europe to the eastern margin of North America, then south to the southern border of North America (Fig. 3-1). This migration route is possible as Western Europe and the eastern margin of North America were connected during the Cenomanian-Turonian.

5. Extinction

The restricted temporal range (Lower-Upper Cenomanian) observed for dolichosaurs in Europe and the Middle East is likely an artefact of the focus on fossil collecting in association with the rarity of these animals in the fossil record. However, it is also possible that these small marine squamates suffered extinction or near-extinction during the Cenomanian-Turonian Boundary Event or CTBE (Caldwell and Cooper, 1999). The CTBE was a relatively short-lived (250ka), but major palaeoceanographic event that lead to an extensive faunal turnover (Sepkoski, 1986; Lamolda et al., 1994). It coincides with a maximum transgression at the end of the Cenomanian, but is widely regarded as the consequence of a global 'Oceanic Anoxic Event" (OAE). Evidence for an OAE has been recovered worldwide in the form of widespread deposition of organic rich sediments, and a positive ^{13}C isotope excursion (Scholle and Arthur, 1980; Jenkyns, 1985; de Graciansky et al., 1986; Herbin et al., 1986; Schlanger et al., 1987; Hart and Leary, 1989; Leary et al., 1989; Gale et al., 1993; Uličný et al., 1993; Lamolda et al., 1994; Paul et al., 1994; Paul et al., 1994; Hilbrect et al., 1996; Nederbragt and Florentino, 1999; Wang et al., 2001). It is argued that an increased value of ^{13}C in CTBE sediments

is the result of preferential extraction of ^{12}C from the seawater by marine plankton with ^{12}C never being recycled back into the oceanic reservoir due to widespread burial of the organic carbon during the OAE.

There have been multiple hypotheses devised to explain the cause of the OAE during the CTBE. Ideas range from changing oceanic circulation (Jarvis et al., 1988), to Milankovitch cycles (Lamolda et al., 1994; Paul et al., 1994; Wendler, 2002), and even the step-wise transgression of the paleo-seaways (Uličný et al., 1993; Hilbrect et al., 1996). Whatever the scenario may be, most researchers do agree that some event led to a dramatic increase in nutrient availability in the oceanic reservoir. This abundance of nutrients in the water column caused an explosion in primary productivity, which quickly depleted the nutrients eventually killing off the organisms at an accelerated rate. It was this profusion of decaying matter that lead to an expanded 'Oxygen Minimum Zone' (or anoxic zone), which moved up vertically in the water column during the Cenomanian transgression, penetrating the pelagic zone and causing an OAE.

As eustatic sea level rose during the CTBE, the anoxic waters affected organisms living in or on deep ocean basins, continental slopes, submarine plateaux, and epicontinental seas (Reyment and Bengtson, 1986; Schlanger et al., 1987). A dramatic faunal turnover has been recognized in a variety of marine organisms including rudist bivalves (Steuber and Löser, 2000), inoceramid bivalves (Voigt, 1994), and foraminifera (Lamolda et al., 1994; Wang et al., 2000). Extinction rate calculations across the CTBE suggest that planktonic organisms suffered an extinction rate reaching 50-70%, while benthic forms went as high as 90% (Wang et al., 2001). This level of faunal turnover

suggests that the OAE led to a striking restructuring of the Cenomanian-Turonian oceanic ecosystems.

Dolichosaur population structure would have been greatly affected by the OAE because as marine organisms they were part of the oceanic ecosystem during the CTBE. They were living and foraging within the extensive carbonate platforms that were eventually submerged below the euphotic zone and inundated by anoxic water during the transgression of the paleo-seaways (Jenkyns, 1991; Gušić and Jelaska, 1993). In Europe and the Middle East, dolichosaurs do not appear in the fossil record after the CTBE; related marine squamates, such as aigialosaurs and limbed snakes (i.e., Pachyrhachis) that were occupying a similar ecological niche, also disappear from the fossil record during this period. This restriction of dolichosaurs (and similar marine squamates) to the Cenomanian of Europe and the Middle East may be causally linked to the end-Cenomanian extinction. The Turonian record of dolichosaurs from North America may be representative of those taxa that evaded the CTBE by virtue of earlier migrations.

PALEOBIOLOGY

Body Structure

1. General Anatomy

1.1 Dolichosaurus longicollis (Fig. 3-3A)

The head in Dolichosaurus is poorly known; however, the mandible is shallow, elongate, and pointed anteriorly, and possesses a highly mobile intramandibular joint within the jaw ramus. There are at least 19 cervical vertebrae with large posteriorly placed hypapophyses and unfused peduncles (Fig. 3-4A). Not all elements of the limbs

are preserved, but the forelimb is observably shorter and less robust than the hind limb. The trunk is laterally compressed and is composed of at least 32 vertebrae with long, slightly curved ribs and short neural spines. Zygosphenes and zygantra are well developed throughout the cervical and dorsal vertebrae (Fig. 3-4A). There are two sacral vertebrae. The tail is laterally compressed and composed of at least 32 caudal vertebrae with long neural spines and chevrons (Owen 1850; Caldwell, 2000).

1.2 Coniasaurus crassidens and C. gracilodens (Fig. 3-3B)

In Coniasaurus the snout is elongate anterior to the orbits and the skull is generally triangular in shape. The jaws have a shallow profile and display a heterodont dentition. The teeth are elongate, pointed and recurved anteriorly, and swollen and bulbous posteriorly (Fig. 3-4B). There is a highly mobile intramandibular joint within the jaw ramus and the anterior symphysis between the dentaries is loose and mobile. Only fourteen dorsal vertebrae have been documented, all with short neural spines, zygosphenes, and zygantra. The neck, limbs, and tail in Coniasaurus remain unknown (Owen, 1850; Caldwell and Cooper, 1999; Caldwell, 1999b).

1.3 Aphanizocnemus libanensis (Fig. 3-3C)

The skull in Aphanizocnemus is generally triangular in shape. It is elongate with a shortened facial region and a wide occipital region. Dorsoventrally, the skull is fairly shallow and a C-shaped quadrate is present. A mobile intramandibular joint within the jaw ramus is evident. The neck is composed of 10-11 cervical vertebrae with very low neural spines and well-developed hypapophyses. The limbs are very small with parallel

epipodials; however, the forelimb is slightly longer than the hind limb, a result of the strongly regressed tibia. The manus and pes are greatly elongated. The trunk is cylindrical in cross-section and consists of 25 dorsal vertebrae with simple median neural ridges, zygosphenes, and zygantra. Two sacral vertebrae are preserved. The tail is laterally compressed and composed of 141 caudal vertebrae with long neural spines and chevrons (Dal Sasso and Pinna, 1997).

1.4 Acteosaurus tommasinii (Fig. 3-3D)

The head is not preserved in Acteosaurus. The neck is composed of at least 8 cervical vertebrae with long, low neural spines. Both pairs of limbs are reduced in size, with parallel epipodials; however, the forelimb is significantly smaller than the hind limb. The manus and pes are greatly elongated. The trunk is laterally constricted and consists of 27 dorsal vertebrae with low neural ridges and gracile ribs. There are two sacral vertebrae. The posterior part of the tail is missing, but in its current state it is laterally compressed and composed of at least 17 caudal vertebrae with long neural spines and chevrons (Meyer, 1860).

1.5 Eidolosaurus trauthi (Fig. 3-3E)

Only the posterior region of the skull is preserved in Eidolosaurus. Based on its overall appearance the head is relatively small, narrow and generally triangular in shape, with a C-shaped quadrate. Eleven cervical vertebrae with short neural spines compose the neck region. The forelimb is smaller than the hind limb and both have distally diverging epipodials. The manus and pes are greatly elongated. The trunk is laterally

constricted and consists of 23 dorsal vertebrae. All dorsal vertebrae and ribs are heavily pachyostotic. Two sacral vertebrae are present. The posterior part of the tail is not preserved; however, in its current condition, the tail is laterally compressed and composed of at least 48 caudal vertebrae with large neural spines and chevrons (Nopcsa, 1923).

1.6 Pontosaurus lesinensis (Fig. 3-3F)

The head in Pontosaurus is triangular in shape. The facial section and postorbital area are approximately the same length. Dorsoventrally, the skull is fairly shallow and a C-shaped quadrate is present. The dentary possesses a highly mobile intramandibular joint within the jaw ramus and the anterior symphysis between the dentaries is loose and mobile. All the teeth on the maxilla and mandible are pointed and recurved (Fig. 3-4C). Twelve cervical vertebrae with well-developed hypapophyses and unfused puduncles create the neck region. The forelimb is reduced, has distally diverging epidodials, and the manus is greatly elongated. The laterally constricted trunk is composed of 28 dorsal vertebrae and ribs that are somewhat pachyostotic. There are two sacral vertebrae. The hind limb and tail in Pontosaurus remain unknown (Kornhuber, 1973; Pierce and Caldwell, 2002).

1.7 Adriosaurus suessi (Fig. 3-3G)

The head in Adriosaurus is triangular in shape and fairly shallow dorsoventrally. The facial section and postorbital area are approximately the same length. Ten to 11 cervical vertebrae with low neural spines create the neck region. The forelimb is smaller

than the hind limb and both have distally diverging epipodials. The manus and pes are greatly elongated. The laterally constricted trunk is composed of 29 dorsal vertebrae with low neural spines. All the dorsal vertebrae and ribs are heavily pachyostotic. Zygosphenes and zygantra are well developed throughout the cervical and dorsal vertebrae. There are two sacral vertebrae. The laterally compressed tail consists of about 65 caudal vertebrae with long neural spines and chevrons (Seeley, 1881; Lee and Caldwell, 2000, 2002).

2. Aquatic Adaptations

The evolutionary transition from terrestrial to aquatic environments usually results in the restructuring of an animal's anatomy; the body becomes more streamlined and the typical 'load bearing' limbs are modified to assist in aquatic locomotion (e.g. mosasaurs, ichthyosaurs, and whales). The body structure observed in dolichosaurs clearly indicates that these animals evolved towards an aquatic lifestyle. Overall, their body form consists of a long head, neck, body, and tail (Fig. 3-3). Furthermore, the limbs have become significantly reduced. This general body appearance is comparable to that of nothosaurs and pachypleurosaurs, small, aquatic sauropterygians that inhabited lagoons and offshore environments in the Middle and Upper Triassic (Caldwell and Cooper, 1999; Rieppel, 2000). Moreover, except for the limbs, this elongated body form is similar to that observed for Cretaceous limbed marine snakes (Lee and Caldwell, 1998; Lee et al., 1999; Tchernov, 2000) and modern sea snakes.

Dolichosaurs retain numerous skeletal characteristics that indicate an amphibious way of life. The head and neck region are both dorsoventrally constricted and light in

build. This body form can be correlated with movement in an aquatic environment. Flattening the anterior region of the skeleton produces a more streamlined body form and reduces drag while accelerating through an aqueous medium (Scanlon et al., 1999).

The body and tail are both laterally compressed. The dorsal ribs project laterally from the vertebral centra for a short distance before turning ventrally creating a deep, narrow body. Moreover, the caudal vertebrae possess long neural spines and chevrons that produce an oar-like tail. Lateral compression in this manner is also observed in some mosasaurs, pachyophiids, and modern sea snakes and is consistent with an aquatic mode of life.

The forelimbs and the hind limbs are both substantially reduced in size. The dimensions of the propodials (humerus/femur) and epipodials (radius/ulna and tibia/fibula) are smaller than the manus and pes. The epipodials diverge distally and the manus and pes are well developed. Consequently, the limbs, manus, and pes are broad and would have served as effective paddles during aquatic locomotion (Lee and Caldwell, 2000).

Some dolichosaurs show skeletal pachyostosis that results from a thickening of the periosteal bone. Pachyostosis in dolichosaurs is manifested in the middle region of the vertebral column. In this region the vertebrae and proximal portions of the ribs are swollen. This anatomical adaptation is usually restricted to secondarily aquatic vertebrates (reptiles and mammals), and functions to create neutral buoyancy in shallow diving animals by counteracting the buoyancy created by the air filled lungs (Scanlon et al., 1999; Lee and Caldwell, 2000).

3. Facultative or Obligatory

Facultative organisms can survive in a variety of environmental conditions, while obligatory organisms are confined to a particular suite of environmental parameters. In the fossil record, organisms can be found in sediments that do not necessarily represent the habitat that was used during life. Therefore, the distinction between facultative and obligatory extinct animals is not based purely on sedimentological data, but also on the general anatomy of the organism. The anatomy of facultative animals is usually designed to exploit multiple habits. Conversely, the anatomy of obligatory animals is usually highly specialized to very specific habitat.

Facultative marine lizards (i.e., aigialosaurs) have large limbs and girdles that are fully ossified with well-defined articulating surfaces. The humeral-scapulocoracoid is constructed in such a way as to resist vertical dislocation of the humerus by joint loading during the impact phase of terrestrial locomotion. The glenoid fossa on the scapulocoracoid is directed laterally and the deltoid and pectoral tuberosities on the humerus are large. In contrast, obligatory marine lizards (i.e., mosasaurs) have limbs and girdles that are reduced in size and articular surfaces that are often rough and poorly developed. The glenoid fossa of the scapulocoracoid is directed posteroventrally and the humeral tuberosities are reduced. These observed differences in the limbs and girdles of obligatory marine lizards are due largely to the absence of dislocative joint loading forces that are associated with supporting one's body weight during terrestrial locomotion (Caldwell et al., 1995).

In general, the limbs and girdles of dolichosaurs have become reduced and modified. While the glenoid fossa of the scapulocoracoid is directed laterally, the

humeral tuberosities are small, and the articular surfaces (e.g., the olecranon process of the ulna) have become reduced. Nonetheless, the degree of reduction is nowhere near that observed in mosasaurs. Therefore, dolichosaurs appear to be intermediate in a linear series that describes active terrestrial locomotion (aigialosaurs) and fully aquatic habits (mosasaurs) (Fig. 3-5). In this sense, dolichosaurs may have had the ability to move on both land and in water; however, their anatomy clearly indicates that they had become more dependent on aquatic locomotion than other facultative marine lizards.

Locomotion

1. Swimming Mode

The long, thin, and tapering body and tail of dolichosaurs is consistent with anguilliform (category 3 of Carroll, 1985) swimming (Caldwell and Cooper, 1999; Caldwell, 2000; Lee and Caldwell, 2000). Specifically, dolichosaurs probably moved in an axial undulatory to axial subundulatory fashion. In axial undulation to subundulation, the anterior portion of the body is held straight and rigid to reduce drag and to limit movement in a zigzag fashion, while the posterior region maintains a high degree of flexibility (Lingham-Soliar, 1991; Massare, 1994). This type of swimming is usually associated with locomotion in a labyrinthine habitat, for example among rocks, within thick vegetation, or along muddy bottoms (Carroll, 1985).

In association with the general body proportions, the dolichosaur vertebral column also would have supported movement in an anguilliform manner. Dolichosaurs, like other pythonomorphs (mosasauroids, pachyophiids and modern snakes) possessed tight accessory vertebral articulations known as zygosphenes and zygantra (Fig. 3-4A).

In mosasauroids and snakes, the zygosphenes and zygantra function to reinforce the articulations between vertebrae and to control the mobility of the vertebral column (Lingham-Soliar, 1991; Scanlon et al., 1999). More specifically, it is hypothesized that contraction of epaxial muscles draws successive zygosphene-zygantral facets into close contact thereby restricting lateral movement and forming in effect a horizontal strut (e.g. stiffness anteriorly). In contrast, relaxation of the musculature and release of this tight vertebral association facilitates a greater degree of sinusoidal movement (e.g. mobility posteriorly). Therefore, the presence of zygosphene-zygantral articulations allows movement in an angulliform fashion (Lingham-Soliar, 1991). The zygosphenes and zygantra may have served a similar role during swimming in dolichosaurs.

2. Swimming Behaviour

Although the body proportions of dolichosaurs are most consistent with modern marine snakes, the lack of limbs in marine snakes does not give us any indication of how the paddle-like limbs of dolichosaurs were utilized during swimming. Therefore, the swimming behaviour (slow, medium, and fast swimming) of dolichosaurs can be best modeled after young salt-water crocodiles (Davenport and Sayer, 1989) and modern marine iguanas. Juvenile salt-water crocodiles and marine iguanas are an appropriate modern analogue to draw on since they both move in an anguilliform manner and have paddle-like limbs (though not as small as those of dolichosaurs).

When swimming slowly, dolichosaurs may have relied upon the synchronized ipsilateral (one forelimb and the hind limb on the opposite side) movement of all four limbs (Fig. 3-5A). During the effective stroke the large manus and pes may have been

spread out and pushed backwards at right angles to the direction of swimming. At the end of the effective stroke the manus and pes would collapse and the limb would have been brought forward in a recovery stroke. This low pace paddling, a typical tetrapod pattern, would have allowed the animal to maintain a slow, but steady speed.

Medium speed swimming in dolichosaurs could have been accomplished through the combined action of the tail and limbs (Fig. 3-5B). The limbs would have continued a synchronized ipsilateral movement, while a propulsive wave passed rearwards along the tail with progressively increasing amplitude.

Fast swimming in dolichosaurs was probably achieved by the propagation of lateral waves along the body and tail, all limbs being held immobile and close to the body to minimise drag (Fig. 3-6A). The tail would have provided the bulk of the propulsion, even though the propulsive wave would have originated in the body just anterior to the pectoral girdle. To counteract rolling and yawing during a rapid shallow dive, the hind limbs would have been held parallel to the body axis as the forelimbs shifted positions; during the descent the forelimbs would have trailed in a raised position (Fig. 3-6B), while during the ascent they would have trailed below the body creating hydrodynamic lift (Fig. 3-6C).

3. Terrestrial Locomotion

Movement on land by dolichosaurs was probably rare. Elongation and lateral compression of the body along with small limbs would have made for slow, clumsy and laborious terrestrial locomotion (Lee and Caldwell, 2000). If dolichosaurs utilized their small limbs on land, terrestrial locomotion was probably accomplished in much the same

way as elongate salamanders (O'Reilly et al., 2000) and other typical tetrapod lizards (Pough et al., 1998). At slow speeds, lateral waves would have propagated down the body while one limb progressed forward, the other three feet remaining in contact with the substrate. If the animal needed to escape rapidly, there could have been a shift to a trotting gait that leaves only two feet on the substrate at any given time. This would create an ipsilateral movement of the limbs similar to the pattern used for slow swimming.

Nevertheless, an anguilliform or serpentine (limbless) terrestrial movement by dolichosaurs cannot be ruled out. For instance, some modern burrowing lizards have similar body proportions to dolichosaurs. They are greatly elongate and have highly reduced limbs. These burrowing lizards only use their small limbs to prop themselves up or to manoeuvre over obstacle during slow speeds. During rapid movement, these modern elongate lizards resort to serpentine locomotion by holding all limbs immobile and close to the body (Cogger, 2000). A similar snake-like movement may have been employed by dolichosaurs. In fact, a legless approach to terrestrial locomotion may have been more efficient than attempting to support their elongate bodies on such small limbs.

Terrestrial Behaviour

1. Basking And Reproduction

Dolichosaurs may have departed from their aqueous environment to either bask in the sun or lay eggs. Heating up the body through solar activity is a typical reptilian behaviour that is used to increase metabolic rate. Dolichosaurs may have done so to digest their food or to increase body temperature in order to forage. However, it has been

observed that modern sea snakes do not need to leave the water in order to 'heat up'. By living in warm waters the body temperature of sea snakes remains fairly constant; consequently, basking is rare and is usually accomplished by resting at the water's surface (Heatwole, 1999). Dolichosaurs may also have been able to maintain a relatively constant body temperature by living in the warm shallow waters of the Northern Tethys Region and the southern Western Interior Basin. Nonetheless, as indicated by their paleobiogeographical distribution, they also inhabited relatively temperate waters in the Anglo-Paris Basin and the mid-west of the Western Interior Basin. Animals of this small size living in these cooler bodies of water may have needed to leave their aqueous environment in order to bask in the sun (e.g., marine iguanas).

In terms of reproduction, it is unknown whether dolichosaurs were oviparous (egg layers) or viviparous (live bearers). If they were oviparous it would have been necessary to venture out onto land in order to deposit their eggs; however, if they were viviparous they would have given birth underwater. Recently there was a report of viviparity in an aigialosaur (Caldwell and Lee, 2001). The exceptional remains of a gravid female were described with at least four advanced embryos distributed along the truck region. The embryos were oriented in such a way that would have caused them to be born tail first, thus reducing the possibility of drowning. Knowing that aigialosaurs and dolichosaurs are phylogenetically closely related (Dal Sasso and Pinna, 1997; Caldwell, 1999a; 2000; Lee and Caldwell 2000; Pierce and Caldwell, 2002, Chapter 2) it is not implausible to imagine that dolichosaurs also gave birth to live young; however, more evidence is needed.

Feeding And Foraging

1. Diet And Niche Partitioning

The skull anatomy observed in dolichosaurs is clearly that of a predator. In all cases the skull is lightly built and triangular in shape tapering to a point anteriorly. The maxillae and mandibles are both gracile, elongate bones, with shallow lateral profiles. The dentition is of two types: (1) all the teeth are laterally compressed, pointed, and recurved (Fig. 3-4C); and (2) teeth are heterodont being elongate, laterally compressed, and pointed anteriorly, then gradually becoming robust and bulbous posteriorly (Fig. 3-4B). The sleekness of the skull coupled with the dentition indicates that dolichosaurs were carnivorous animals probably feeding on a variety of marine vertebrates (fish) and invertebrates (echinoderms, bivalves, and crustaceans) that inhabited the vast carbonate platforms of the Upper Cretaceous (Caldwell and Cooper, 1999).

The close temporal and spatial relationship among the different dolichosaur species with other pythonomorphs (i.e., aigialosaurs and primitive snakes) suggests that these animals were able to partition resources in a shared environment. Niche partitioning may have been accomplished through differences in feeding habits and prey selection (Caldwell and Cooper, 1999). For example, different species of modern sea snakes are able to coexist in a limited coastal environment by foraging in various sub-niches (e.g. inshore near bottom, rock dweller, reef dweller, and pelagic) and feeding on a diverse array of prey items (e.g. eels, bullet-shaped fishes, vertically or laterally oversized fishes, and fish eggs) (Voris, 1972; Voris and Voris, 1983). This type of niche partitioning may have also been the case for Upper Cretaceous pythonomorphs.

Just how niche partitioning was accomplished among dolichosaurs, aigialosaurs and primitive snakes is unknown. Based on body size, aigialosaurs were probably able to actively hunt and kill larger prey items than dolichosaurs and primitive snakes. On the other hand, dolichosaurs and primitive snakes were of similar body proportions; however, the greatly expanded oropharyngeal gape of primitive snakes probably allowed them to forage on larger prey items also. This is evident in the remains of a large pyconodont fish preserved within the abdominal region of the legged snake Pachyrhachis (Scanlon et al., 1999). In contrast, dolichosaurs would have been feeding on relatively small animals compared to both aigialosaurs and primitive snakes.

2. Prey Size

The overall body proportions (i.e., long and narrow) observed in dolichosaurs implies that they fed on relatively small prey items; however, two distinct features of the skull suggest that these animals were able to greatly increase their potential oropharyngeal gape. Dolichosaurs possess a highly mobile intramandibular joint within each jaw ramus (Fig. 3-4B) and the anterior symphysis between the dentaries was loose and mobile (similar to mosasauroids, pachyophiids, and snakes). These features of the mandible combine to increase the gape (Cundall, 1995). The lower jaw bows outwards at the intramandibular joint; this causes the two dentaries to open at a more obtuse angle, and such movements are accommodated by the loose mandibular symphysis. The two rami of the lower jaw bulge far apart and allow the passage of larger food items into the oropharyngeal area (Lee et al., 1999; Scanlon et al., 1999).

The quadrate of dolichosaurs is reminiscent of the typical C-shaped quadrate observed in mosasaurs and aigialosaurs. In this respect, dolichosaurs most likely developed a similar condition of streptostyly to that proposed for mosasaurs (Kauffman and Kesling, 1960; Russell, 1964). Dolichosaur quadrates were probably loosely attached to the quadratic ramus of the pterygoid and were independently moveable. They would have been able to pivot anteroposteriorly and splay laterally within the cotylus of the suspensorial process of the braincase. This dynamic movement of the quadrate would cause an increase in the potential gape and permit the passage of larger food items in the oropharyngeal area.

3. Predation

Based on anatomy, dolichosaurs were relatively slow swimmers with a limited range of manoeuvrability. Therefore, these animals were probably not pursuit predators, but rather ambush predators inhabiting shallow reefs and lagoons similar to modern sea snakes and the primitive snake Pachyrhachis (Scanlon et al., 1999). Dolichosaurs, therefore, could have employed the two main prey capture techniques known for modern sea snakes and proposed for Pachyrhachis (Heatwole, 1999; Scanlon et al., 1999).

The first strategy is foraging within small crevices and cornering prey items. To investigate small nooks and crannies sea snakes have become microcephalic: their anterior bodies are extremely small (neck girths are only about 2cm) relative to their posterior region. This morphology permits the anterior end of the animal to enter and investigate narrow burrows and crevices in search of prey (Voris and Voris, 1983; Scanlon et al., 1999). The small head and long slender neck of dolichosaurs is consistent

with this mode of feeding. Furthermore, the dolichosaur vertebral column possesses zygosphene-zygantral articulations (see above); these accessory articulations would have facilitated a higher degree of manoeuvrability of the neck during exploration of complex structured habitats such as reefs, rocks, and rubble (Lingham-Soliar, 1991).

The other dominant prey-capture method employed by sea snakes is cruising through prey-rich water and striking at any individual that comes within range. The predatory strike is accomplished by opening the mouth and rapidly swinging the head sideways. When a prey item is captured, the head is held in a J-shaped position (towards the tail) while the snake continues to swim forwards. The water flow helps keep the victim properly aligned during swallowing.

Recently, a new type of prey capture in aquatic snakes was observed (Smith et al., 2002). The tentacled snake, Erpeton tentaculatum, is a freshwater piscivorous animal that employs a unique predatory strike to capture its prey. As the snake submerges itself beneath the water, its prehensile tail often, but not always, wraps around an object, its body becomes rigid and is held out straight, and its head turns posteriorly thereby forming a J-shaped bend in the neck. The snake waits in this J-shaped posture for a fish to move into the very narrow 'window' between the turned head and the body. From this position an extremely rapid predatory strike is engaged. The head turns and travels posteriorly towards the fish with the mouth protracted. The fish is secured on buccal teeth and is quickly swallowed by unilateral displacement of the jaws.

The predatory strikes employed by both sea snakes and the tentacled snake are reasonable modern analogues with respect to dolichosaur prey capture techniques. The ability to perform a predatory strike is consistent with dolichosaur vertebral anatomy. In

order to accomplish a strike, dolichosaurs would have relaxed the epaxial muscles of the neck allowing the zygosphene-zygantral articulations to provide sufficient lateral flexibility (Scanlon et al., 1999); this would have allowed the J-shaped posture to be achieved. Additionally, like all modern snakes that strike, dolichosaurs possess a series of hypapophyses on the cervical vertebrae (Fig. 3-4A). The presence of hypapophyses implies an ability to strike by rapid release of pre-tensed lateral curves in the neck region (Mosauer, 1935; Gasc, 1974; Scanlon et al., 1999).

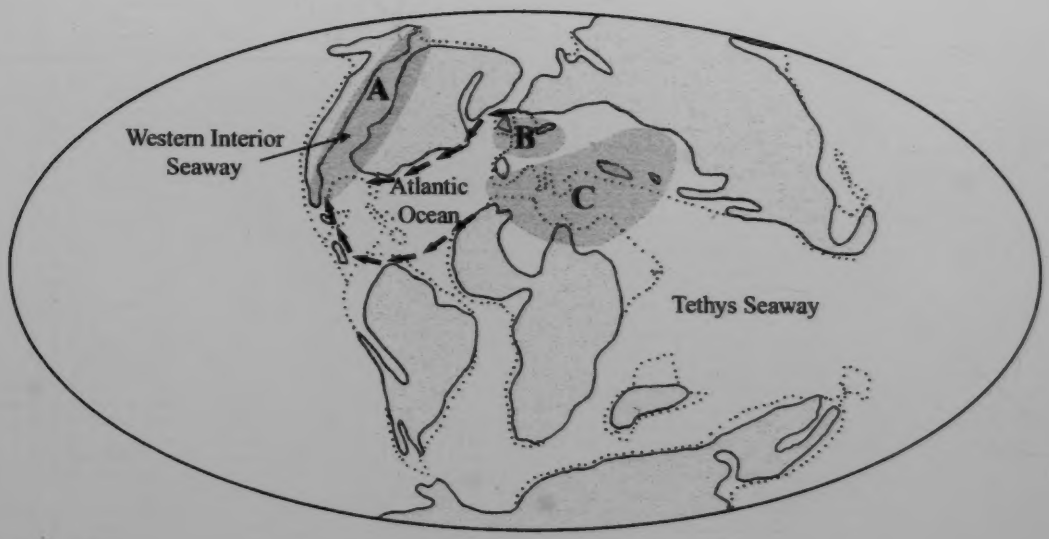
SUMMARY AND CONCLUSIONS

Dolichosaurs were a geographically wide spread group of marine lizards that inhabited the vast epicontinental seas of the Upper Cretaceous from the Lower-Middle Cenomanian to Upper Turonian. They appear to have been generalists occupying a broad range of environmental parameters. Their fossil remains are found in tropical to temperate settings and from near shore to offshore environments. Dolichosaurs appear to have originated in the Tethys Seaway in the Lower-Middle Cenomanian and migrated west into the Western Interior Seaway in the Upper Cenomanian following the dominant westward flow of the Tethys-SuperTethys Seaway.

Dolichosaurs were small elongate marine lizards that developed a number of anatomical features associated with an amphibious lifestyle. They were anguilliform swimmers that utilized both their elongate bodies and tails and their paddle-like limbs to generate propulsive forces. Based on body proportions, terrestrial locomotion by dolichosaurs was probably rare and laborious, but might have been necessary to either bask in the sun or to lay eggs. Dolichosaurs were predatory animals that fed on a variety

of relatively small marine vertebrates and invertebrates. They were not pursuit predators, but rather ambush predators that may have foraged within small crevices and/or utilized a predatory strike.

FIGURE 3-1. Cenomanian Paleocoastline Map (98-93 mys). **A**, Western Interior Basin; **B**, Anglo-Paris Basin; **C**, Northern Tethys Region. Light grey designates Cenomanian land masses. Dotted lines outline the margins of modern coastlines. Arrows indicate the possible migration routes dolichosaurs could have utilized in order to disperse to North America.


A
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Western Interior
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Ocean
Tethys Seaway

CANADIAN THESIS
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PIERCE, Stephanie Elaine
REDESCRIPTION OF PONTOSAURUS LESINENSIS AND THE EVALUATION OF ...

ISBN 0-612-82329-6
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FIGURE 3-2. Cenomanian Map (98-93 mya) showing the paleobiogeographic distribution of known dolichosaur fossils.

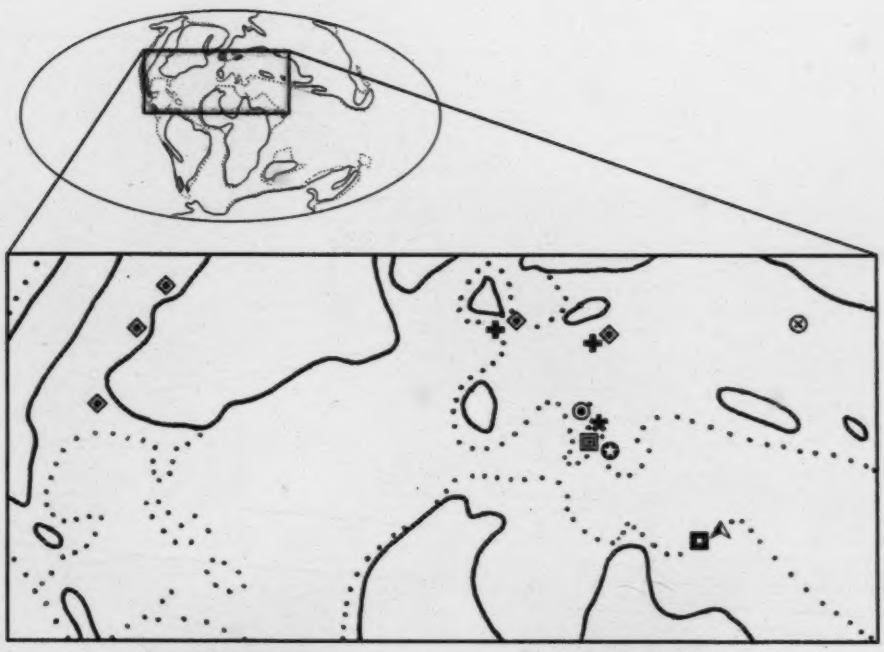
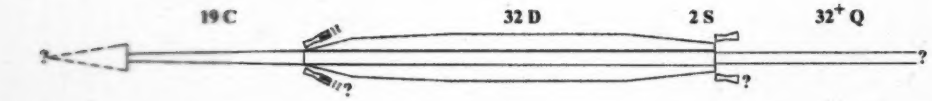
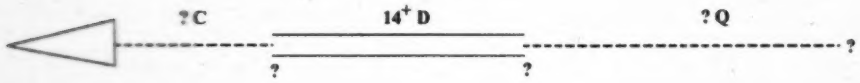

Coniasaurus
Dolichosaurus
Unidentified
Aphanizocnemus
MSNM V3662
Adriosaurus
Acteosaurus
Eidolosaurus
Pontosaurus

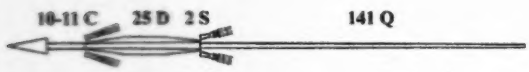
FIGURE 3-3. The overall anatomical proportions of the seven known dolichosaur genera. **A**, Dolichosaurus; **B**, Coniasaurus; **C**, Aphanizocnemus; **D**, Acteosaurus; **E**, Eidolosaurus; **F**, Pontosaurus; **G**, Adriosaurus. Abbreviations: C–cervical vertebrae; D–dorsal vertebrae; S–sacral vertebrae; Q–caudal vertebrae; ?–uncertain. Scale bar = 50mm.


19 C
32 D
2 S
32+ Q
?
?
?
?

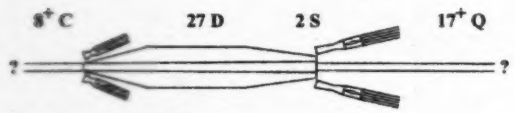
A


? C
14+ D
? Q
?
?
?

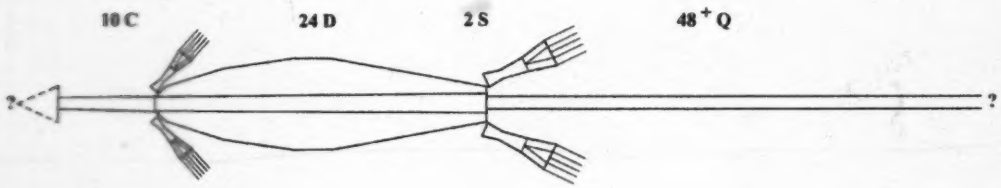
B


10-11 C
25 D
2 S
141 Q

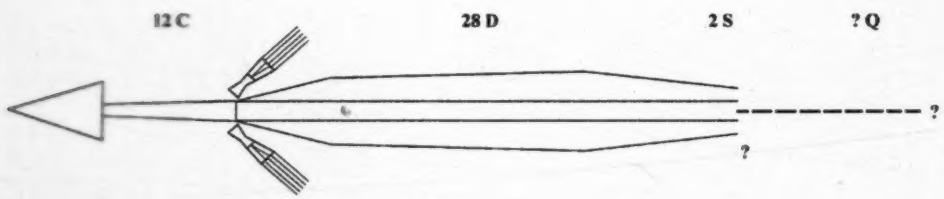
C


8+ C
27 D
2 S
17+ Q
?
?

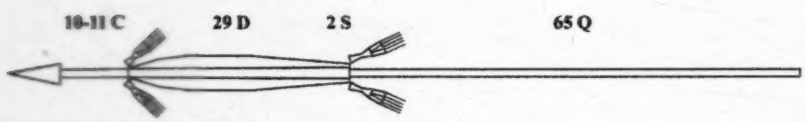
D


10 C
24 D
2 S
48+ Q
?
?

E

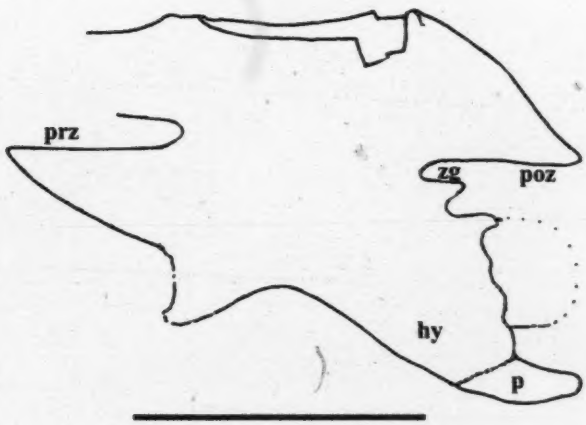

12 C
28 D
2 S
? Q
?
?

F

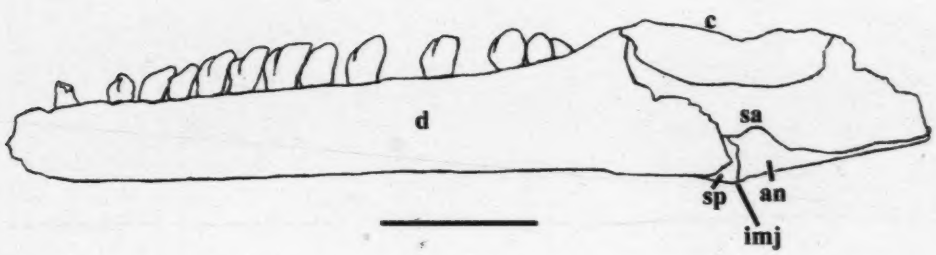

10-11 C
29 D
2 S
65 Q

G

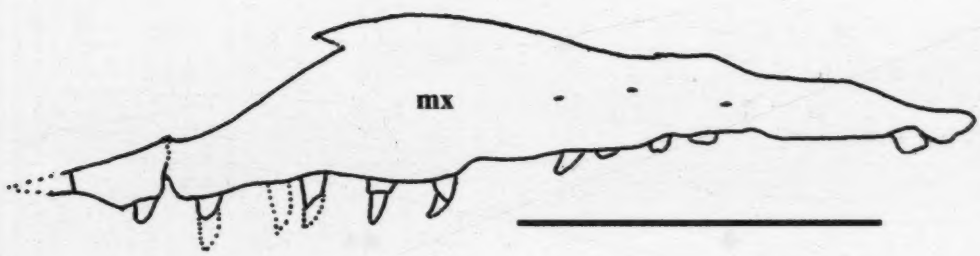
FIGURE 3-4. A, a cervical vertebra of Dolichosaurus showing accessory articulations and a well-developed hypapophysis (modified from Caldwell, 2000). Scale bar = 5mm; **B**, the lower jaw of Coniasaurus showing heterodont bulbous teeth and an intramandibular joint (modified from Caldwell and Cooper, 1999). Scale bar = 10mm; **C**, the maxilla of Pontosaurus showing laterally compressed, pointed, and recurved teeth (from Pierce and Caldwell, 2002). Scale bar = 10mm. Abbreviations: an–angular; c–coronoid; d–dentary; hy–hypapophysis; imj–intramandibular joint; mx–maxilla; p–peduncle; poz–postzygapophysis; prz–prezygapophysis; sa–surangular; sp–splenial; zg–zygantrum.



A



B



C

FIGURE 3-5. A linear comparison between the body proportions of: **A**, a facultative marine lizard Opetiosaurus (aigialosaur); **B**, the dolichosaur Adriosaurus; and **C**, an obligatory marine lizard Clidastes (mosasaur). Dolichosaurs appear to be intermediate between facultative and obligatory marine lizards. Scale bars = 50mm.

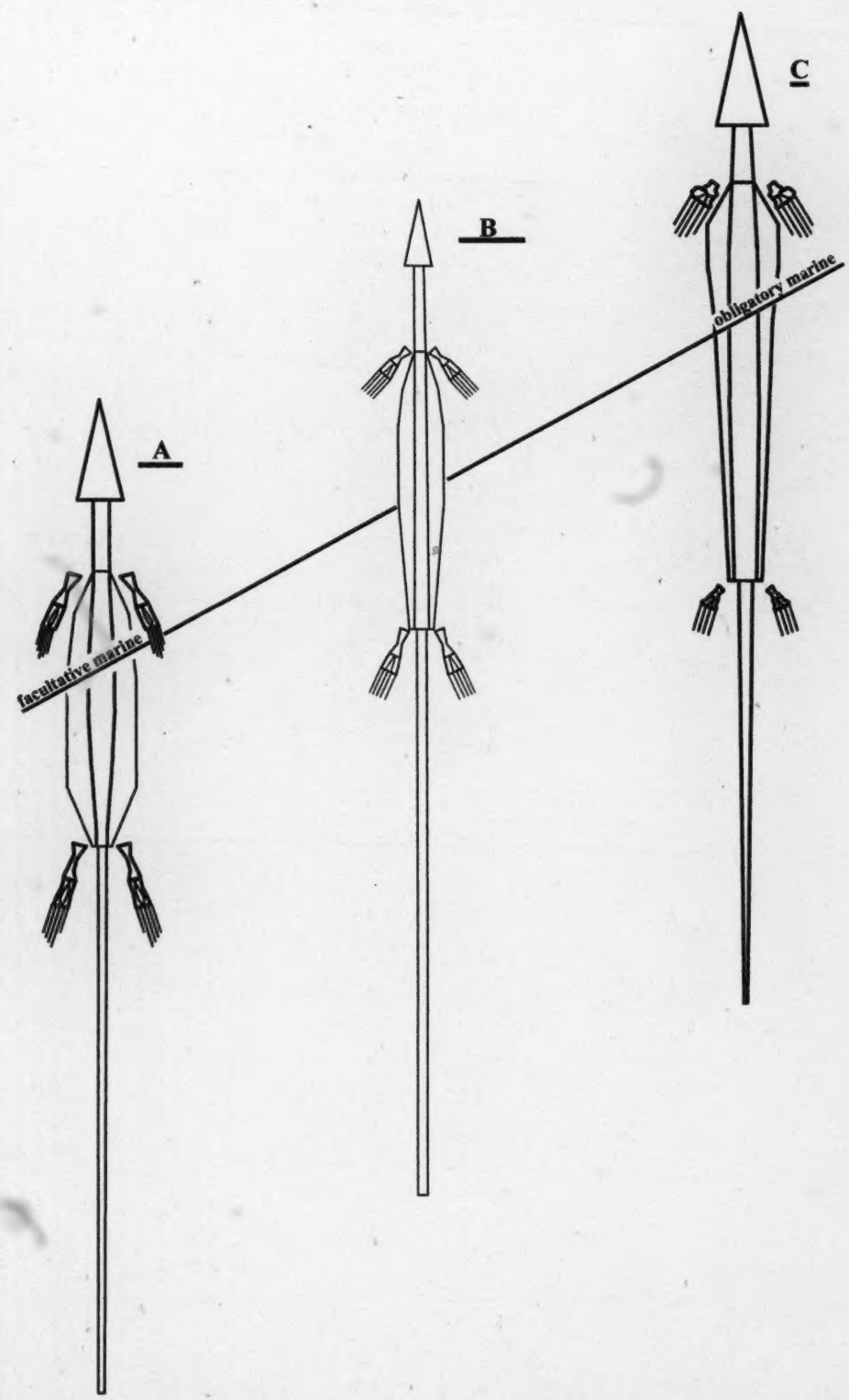
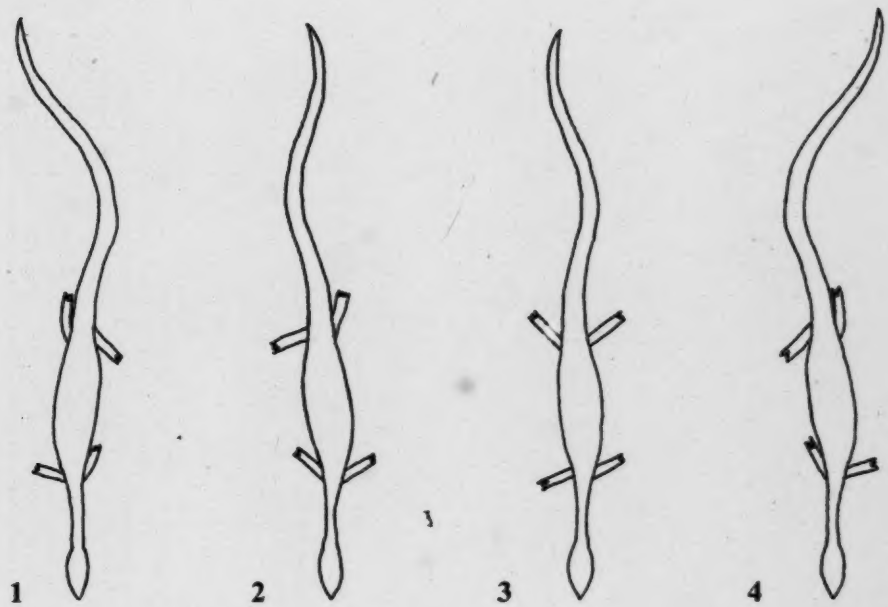

C
B
A
obligatory marine
facultative marine

FIGURE 3-6. Slow and Medium speed swimming behaviours in dolichosaurs. **A**, Slow swimming is accomplished by the synchronized ipsilateral (one forelimb and the hind limb on the opposite side) movement of all four limbs (arrows indicate the direction of limb movement); **B**, Medium speed swimming is accomplished by combining the ipsilateral movement of the limbs with a propulsive wave in the tail (numbers indicate a time progression series).

A

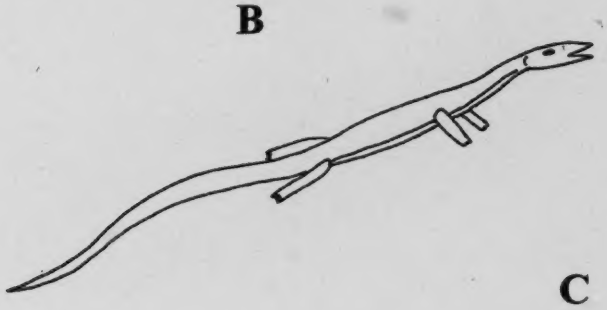


B

FIGURE 3-7. Fast swimming behaviour in dolichosaurs. **A**, Fast swimming is achieved by the propagation of lateral waves along the body and tail, all limbs being held immobile and close to the body to minimise drag; **B**, During a rapid descent, the forelimbs would have trailed in a raised position to counteract rolling and yawing; **C**, During a rapid ascent, the forelimbs would have trailed below the body creating hydrodynamic lift.

A

B



C

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GENERAL CONCLUSION

CONCLUSIONS OF THESIS

My thesis represents the first comprehensive analysis of the anatomy, phylogeny, and paleoecology of dolichosaurs. Thus, it documents and analyses aspects of dolichosaurian evolution, which were previously poorly represented in the literature. As such, the conclusions presented here can be used as a template for future research.

My reassessment of the poorly known dolichosaur Pontosaurus lesinensis produced an extensive redescription of the animal (Chapter One). The redescription both significantly modifies and expands on the original study (Kornhuber, 1873), which was very brief and inaccurate in many respects. However, there still exists a large amount of missing anatomical information, as the posterior portion of Pontosaurus has yet to be discovered. A cladistic analysis of the affinities of Pontosaurus (Chapter One) determined that it is more closely related to other dolichosaurs (Nopcsa 1903) than to aigialosaurs (Kramberger, 1892) or the modern genus Varanus (Kornhuber, 1873). Additionally, the cladistic analysis further reinforced the assertion (Lee and Caldwell, 2000) that dolichosaurs are a non-monophyletic assemblage that form successive sister taxa to snakes.

Based on my own analysis of dolichosaur anatomy and interrelationships (Chapter Two), it appears as though dolichosaurs are a non-monophyletic group that form successive sister taxa to snakes. Therefore, this phylogenetic pattern has been recovered in three studies (Lee and Caldwell, 2000; Chapter One; Chapter Two) and seems to be well supported. As a consequence, the family Dolichosauridae has been modified to include only Dolichosaurus longicollis, Coniasaurus crassidens, and Coniasaurus gracilodens. Additionally, it appears as though snakes are nested deeply within a

radiation of elongate, limb reduced, marine squamates. Therefore, this study continues to provide support for the marine origins hypothesis of snake origins and seems to suggest that marine habits are primitive for snakes.

The investigation of dolichosaur paleoecology (Chapter Three) was made possible through understanding both their anatomy and phylogeny (Chapter One and Chapter Two). Because dolichosaurs occupy such a crucial phylogenetic position to snakes it is important to recognize aspects of their paleoecology, as this information may be central to understanding the paleoecology of snake origins. Through my comprehensive geological and paleobiological examination of dolichosaurs, a variety of paleoecological conclusions were established. Dolichosaurs were found to be a geographically wide spread group of marine lizards. They appear to have been generalists occupying a broad range of environmental parameters that consist of tropical to temperate settings and from near shore to offshore environments. Dolichosaur anatomy is consistent with an amphibious lifestyle and appears to be very similar to Upper Cretaceous limbed marine snakes. They were predatory animals that fed on a variety of relatively small marine vertebrates and invertebrates. Their anatomy suggests that they were anguilliform swimmers that ambushed their prey by either foraging within small crevices and/or utilized a predatory strike.

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